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Adult Marbled Murrelet *(Brachyramphus marmoratus)*
at entrance to nest cavity near Port Chatham, Alaska, 3 July 1981.
Photo by Stuart Johnston.

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CAVITY-NESTING MARBLED MURRELETS

STUART JOHNSTON AND HARRY R. CARTER

In a recent paper (Day et al. 1983), a nest of a Marbled Murrelet (*Brachyramphus marmoratus*) was documented that had been found by S. Johnston on 2 July 1981 near Port Chatham, Alaska (see also Gibson 1981). This was the sixth definite nest of this species found in North America and the fifth definite ground nest (Carter and Sealy 1983). The nest was only briefly described as Johnston was unable to supply further information to R. H. Day at that time. Thus, little attention was given to the fact that this was the first definite nest to be located in a cavity. The cavity was described in Day et al. (1983) as "a small grotto." The cavity was about 50 cm deep, 20 cm across, and 20 cm high at the entrance (estimated from a field drawing and photographs). An incubating bird was flushed from the cavity on 2 July, permitting Johnston and other members of the British Aleutian Islands Expedition 1981 to examine closely the egg and nest site. The ground color of the egg was a bright pale green, which is characteristic of most Marbled Murrelet eggs (Kiff 1980, Day et al. 1983). The egg was covered by dark brown, slaty, and lilac spots that were clustered mainly at the large end. Although dark green mosses and grasses and pale lichens grew at the entrance to the cavity, no nest was evident and the egg rested on bare rock.

On 3 July, Johnston observed an adult (in alternate plumage) incubating the egg. The incubating bird was about 30 cm from the entrance (i.e., near the back) of the cavity, where it would be protected from rain and most winds. It faced outward and at times held its head below the high point of the back in a flattened posture (see Simons 1980). It was observed and photographed from 2–8 m for about 5 hr. It opened and closed its eyes (possibly dozing on the nest) but otherwise remained motionless. It finally came to the entrance for about a minute (see Frontispiece) when Johnston accidentally startled it, but it returned and resumed incubating

in the same position. This short glimpse, however, afforded ample time for definite species identification and documenting photographs.

The nest was found at an elevation of about 710 m, about 55 m below the top of a mountain (as reported in Day et al. 1983). This is the highest elevation at which a nest of a Marbled Murrelet has been found. The surrounding area was very rocky alpine habitat with sparse vegetation. The cavity was a hollow in the side of a rock outcrop or "stack," such that the entrance faced to the west and sideways across the south-facing slope. This outcrop was a distinct feature that stood about 1.5 m higher than the rest of the steep slope. Lower on the slope, subalpine vegetation included salmonberry (*Rubus spectabilis*), bracken (*Pteris* sp.), and elderberry (*Sambucus* sp.) up to 2-m high with some alder (*Alnus* sp.) and small spruce (*Picea* sp.). The coastline of Port Chatham, where the slope leveled out, was heavily forested (mainly Sitka spruce, *Picea sitchensis*) but part of this area had been logged recently. The ocean at Port Chatham was clearly visible from the nest site (an aerial distance of 1–2 km), as were the Barren Islands (about 40 km distant) where Marbled Murrelets are also known to nest (Simons 1980, Hirsch et al. 1981).

Marbled Murrelets have been suspected of nesting in cavities by many workers. Native Indians told Grinnell (1897) and Cantwell (1898) that murrelets nested in hollow trees, high on the mountainside in Alaska; other Indians told Dawson (1923) that they nested in burrows on some of the higher slopes of the Olympic Mountains in Washington. C. de B. Green, A. Brooks, and S. J. Darcus reportedly discovered murrelets nesting in burrows on Cox Island, British Columbia, but their evidence has been doubted consistently (cf. Sealy 1974; Kiff 1980; Sealy and Carter, in press). Guiguet (1971) reported that loggers had observed murrelets leaving high cliff faces on Vancouver Island, British Columbia. Although he did not find any birds there the following breeding season, nest sites may have been deserted due to disturbance from logging. The discovery of a nest of a Marbled Murrelet in a cavity near Port Chatham lends greater credence to earlier unconfirmed reports of nests in various types of cavities. Marbled Murrelets are now known to nest on tree branches (Kuzyakin 1963, Binford et al. 1975), on the open ground (Simons 1980, Hirsch et al. 1981, Day et al. 1983), and in cavities. The diverse types of nest sites used by Marbled Murrelets and their solitary-nesting behavior increase the difficulty of finding nests. The ability to use various types of nest sites may prove to be important to future populations if logging continues to remove tree-nesting habitat in many parts of the breeding range (Sealy and Carter, in press).

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COLOR PLATE

Inclusion of the color frontispiece of an adult Marbled Murrelet (*Brachyramphus marmoratus*) at the entrance to its nest cavity has been made possible through an endowment established by George Miksch Sutton (1896–1982). Photo by Stuart Johnston.

Wilson Bull., 97(1), 1985, pp. 4–20

RELATIONSHIPS AMONG SONG ACTIVITY, CONTEXT, AND SOCIAL BEHAVIOR IN THE WARBLING VIREO

DARYL HOWES-JONES

The songs of most passerines are classic examples of a nested hierarchical structure. They can be described at a number of levels where each level is made of components and their relationships, which together form the next higher level (see Simon 1962, Polanyi 1968, Mesarovic and Macko 1969, Dawkins 1976). Examples of levels in song are figures, phrases, songs, bouts, circadian cycles, seasonal cycles, etc. The studies of avian communication that are concerned with the encoding of information and its relationship with context have focussed mainly on changes in structures at the level of song or below (for examples see Marler 1956; Falls 1963, 1969; Smith 1965, 1968, 1977; Morse 1967; Emlen 1972; Armstrong 1973; Catchpole 1973; Kroodsma 1975, 1977; Lein 1978; Smith et al. 1978). Most of the studies on levels above that of song relate changes in song activity to changes in the components that make up song (for examples see Hinde 1958, Thompson 1972, Armstrong 1973, Heckenlively 1976). Numerous factors have been described which influence the amount and rate of singing (Thorpe 1961, Armstrong 1973, Slagsvold 1977). Although certain relationships between changes in song activity with season and context are well known (e.g., mate attraction, territorial behavior, courtship, relationship to the breeding cycle), studies tend to be anecdotal and suffer from a lack of quantitative data (Catchpole 1982). If song is taken as the unit of analysis, do differences in the temporal patterning of song encode different messages, and if so what significance do these changes have on social behavior?

In this study the song activity of the Warbling Vireo (*Vireo gilvus*) in southern Ontario is examined. The purpose is to describe and quantify relationships among cadence, song rate, breeding cycle, and context, and to determine their possible importance in the social behavior of the pair.

METHODS

Warbling Vireos were studied in Cootes Paradise Sanctuary, Royal Botanical Gardens, Hamilton, Wentworth Co., Ontario, from May to August in the years 1975–1977. Vireos were observed in the same time interval each day. During each observation period an attempt was made to record all songs given by the same individual for periods ranging from 20 to 60 min duration. The same birds were followed each day during the season. Song activity was documented on data sheets marked out in minutes and seconds. When nest-building began, an observer remained near the nest and recorded behavior in detail while another

observer followed the male. Since males sang fairly constantly for most of the nesting cycle, their activities could be observed in detail. Birds were not marked, however, individuals could be distinguished in most circumstances based on characteristics of song, behavior, and use of song perches. No male replacements were suspected based on changes in the above characters and in male–female interaction. Males occupying isolated territories were selected to aid observation. Song data presented in this study were gathered on two males in 1975, eight males in 1976, and four males in 1977. One male each in 1975 and 1976 and three males each in 1976 and 1977 occupied similar territories.

I categorized song activity into six contexts based on the proximity of a bird to its mate and nest. I selected the distance of 10 m as the point beyond which a bird was considered distant from the nest or alone (i.e., from its mate) based on observations which I had previously made in 1975 on defence and vocal behavior. The term 'alone' refers to situations where the male is not in the company of its mate.

Contexts include: (1) Male-pre-pair—male is unmated and on territory. (2) Male-alone-distant—male is mated, more than 10 m from the nest, and is alone (includes situations in which the male is alone prior to nest construction). In this context the male either is patrolling the territory or is foraging. (3) Male-alone-near-the-nest—male is within 10 m of the nest and alone. (4) Male-on-the-nest—male is sitting on the nest (i.e., incubating or brooding); female may also be nearby. (5) Male–female-near-the-nest—mates are within 10 m of each other and the nest; female may be sitting on the nest. (6) Male–female-distant—mates together and more than 10 m from the nest; includes situations in which the pair is together prior to nest-building.

These contexts facilitated examination of the possible effects of the proximity of the nest and female on the singing behavior of the male. Interactions between neighbors were not investigated. A male may be influenced by a neighbor's song anywhere in his territory. To reduce effects of neighbor interaction on male song, I did not further consider song given by a territory holder in encounters involving chasing or intense vocal duelling with a neighbor.

Under the term 'song activity' are described the following four variables. '*Cadence*' is the interval in sec between the start of consecutive songs (Reynard 1963). In frequency distributions of cadence, frequency values decreased rapidly at a cadence of about 20 sec. Therefore, I examined cadence up to an arbitrarily selected limit of 30 sec. In the text the term '*singing rate*' excludes 0 songs/min in its calculation, whereas, '*song rate*' includes 0 songs/min in its calculation. '*Time spent silent*' is the number of minutes in a sample with 0 songs/min.

Song output refers to the quantity of song. A '*song bout*' is defined as a group of songs or a song separated by an interval equal to or less than 59 sec, and a '*song bout interval*' as an interval of 60 sec or more between songs (Thompson 1972). Courtship calls are given by females. The contextual relationships of these calls are complex, however, most are associated with courtship activity and function as a precopulatory solicitation signal (Howes-Jones 1982). A preliminary analysis of song data showed that contextual differences in song activity remained independent of changes in the breeding cycle. I, therefore, lumped data on context for the breeding cycle (Table 1).

RESULTS

Description of song.—The song of the Warbling Vireo is complex and highly variable in structure. Song duration averages about 2.5 sec. The figures that make up song are about 0.1 sec in duration and are separated by intervals of about 0.03 sec. Figures are variable in shape, as are patterns

TABLE 1

MEAN AND STANDARD ERROR FOR CADENCE, SINGING SONG RATE, SONG RATE AND TIME SPENT SILENT FOR WARBLING VIREOS IN DIFFERENT CONTEXTS

	Context					
	Male-pre-pair (3)[a,b]	Male-alone-distant (10)	Male-alone-near-nest (10)	Male–female-near-nest (10)	Male-on-nest (10)	Male–female-distant (10)
Cadence (sec)	9.60 ± 0.84	9.38 ± 0.23	9.56 ± 0.26	9.46 ± 0.27	14.03 ± 0.68	13.19 ± 0.34
Range	7.6–10.9	8.5–10.8	8.2–11.1	8.1–10.8	10.7–18.0	11.8–15.4
Singing rate (excludes 0 songs/min)	4.89 ± 0.66	5.07 ± 0.14	5.08 ± 0.24	5.20 ± 0.27	3.27 ± 0.31	2.71 ± 0.14
Range	4.2–6.2	4.4–5.8	4.1–6.4	4.2–6.8	1.9–4.8	2.1–3.3
Song rate (includes 0 songs/min)	4.00 ± 0.52	3.03 ± 0.25	4.75 ± 0.20	4.88 ± 0.31	2.40 ± 0.35	1.26 ± 0.19
Range	3.2–5.3	1.9–4.3	3.9–5.8	3.4–6.5	0.4–4.5	0.4–2.1
Time spent silent (%)	18.6 ± 2.1	39.8 ± 4.3	6.6 ± 1.3	7.1 ± 1.8	30.1 ± 5.9	55.1 ± 5.1
Range	15.1–23.5	18.7–59.1	0–14.6	1.0–21.2	5.3–78.6	31.8–77.2

[a] Number of individuals.

[b] Sample sizes for individuals varied between 52 and 913 for cadence, 24–357 min for song rates, and 24–941 min for time spent silent.

formed by groups of figures. The structure of song and its changes with respect to song activity and context are complex and will not be discussed here (Howes-Jones 1982, unpubl.).

Changes related to context and proximity.—Table 1 summarizes variations in song activity with context. Analysis of variance indicated there were significant differences in cadence, singing rate, and overall song rate among contexts ($F = 20.81$, 20.63, 23.47, respectively; $P < 0.01$). The sum of squares simultaneous test procedure (Sokal and Rohlf 1969) was used to test for differences among contexts.

In general, song activity in the contexts male-alone-near-the-nest, male–female-near-the-nest, male-alone-distant, and male-pre-pair were similar. There were no significant differences ($P > 0.05$) in the above contexts with respect to cadence or singing rate. The frequency distributions for each of the contexts resembled each other for cadence and for singing rate (see distribution for male-near-the-nest in Figs. 1, 2). Among individuals, the most frequent modal values for cadence was 7 and 8 sec (23 of 33 times) and for singing rate between five and seven songs/min (24 of 33 times).

The only difference in song activity among the four contexts was in the continuity of output that became evident when overall song rates were compared. Highest song rates occurred in the contexts male–female-near-the-nest, male-alone-near-the-nest, and male-pre-pair. No significant differences were found ($P > 0.05$). Mean song rate for the context male-alone-distant was significantly lower than the above three contexts ($P < 0.01$). The difference was due to the amount of time birds were silent in each context. When males were near the nest they sang almost continuously (93% or greater), whether they were with the female or not. Unmated males also spent most of their time (81%) singing. By comparison, in the context male-alone-distant males were silent about 40% of the time.

The longest cadences and lowest song rates were recorded in the contexts male–female-distant and male-on-the-nest (Table 1; Figs. 1, 2). For both contexts the mean cadence, singing and overall song rates were not significantly different ($P > 0.05$), but the two contexts were significantly different from the other contexts for all three variables. The difference in cadence between the two groups was approximately 4 sec. Song given on the nest has a regular cadence (Fig. 3C). Songs given in the context male–female-distant tend to be given sporadically (Fig. 3A). In 7 of 10 individuals, the variance in cadence was significantly greater ($P < 0.05$, F-max test) in the context male–female-distant than in the context male-on-the-nest. The average coefficient of variation (c.v.) for male-on-the-nest was lowest among contexts, (38.8, N = 10) whereas, the c.v. for the former context was highest (48.8, N = 10). In the context male–female-distant,

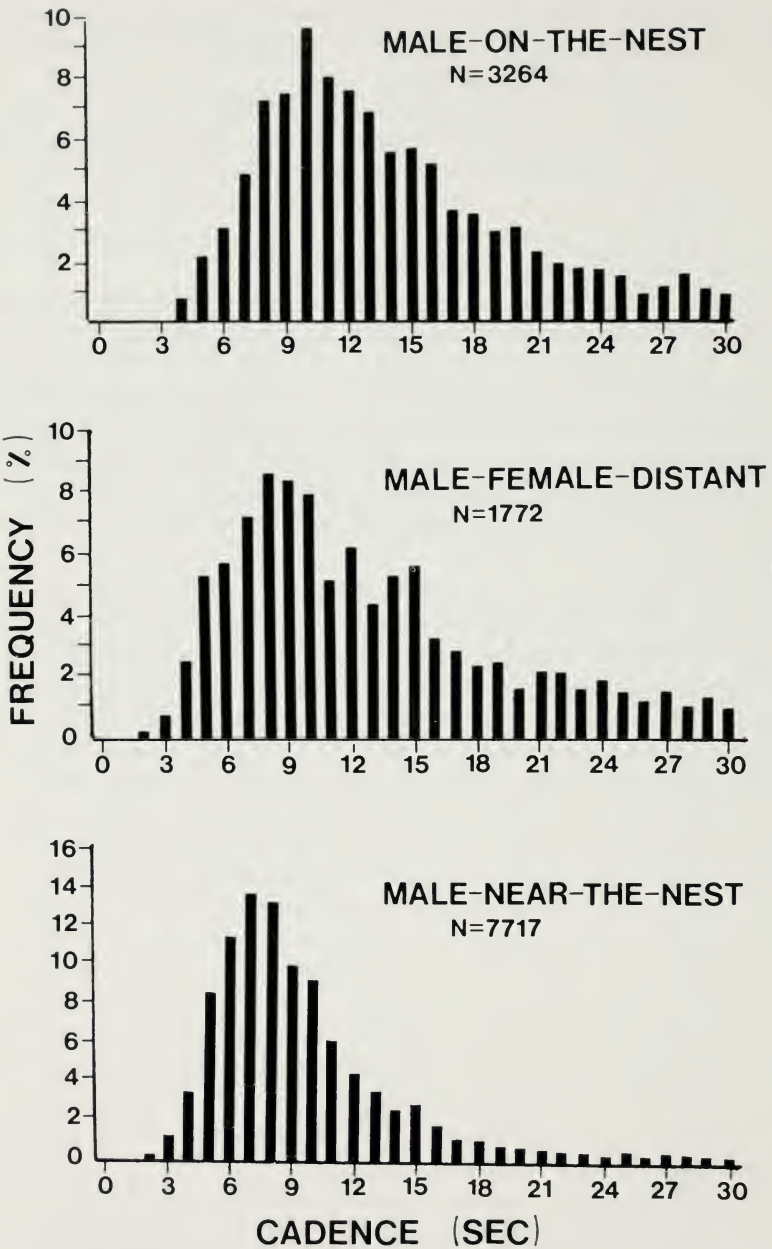

FIG. 1. Frequency distributions of cadence among contexts for 10 males. The context male-near-the-nest includes the contexts male-alone-near-nest and male–female-near-nest.

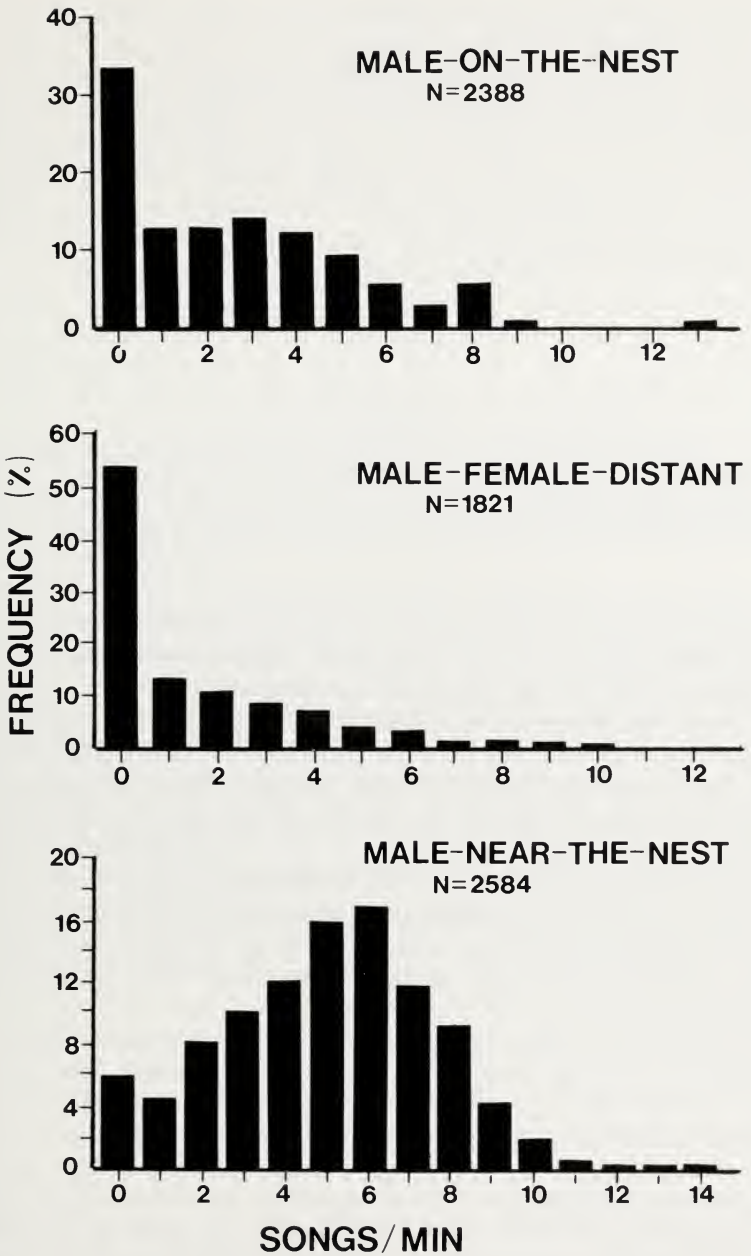

FIG. 2. Frequency distributions of song rate among contexts for 10 males. Male-near-the-nest is the same as in Fig. 1.

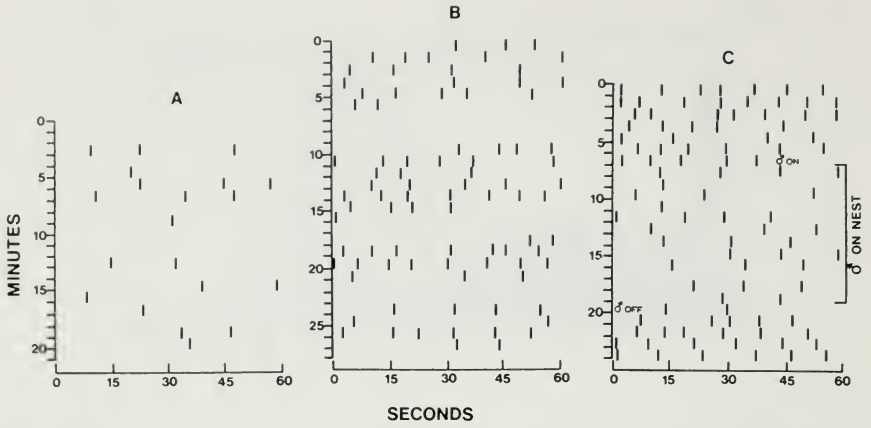

FIG. 3. Examples of song records from the field to demonstrate typical differences in the temporal patterning of song with context. Each mark denotes a song. Patterns were taken from different males. (A) Male–female-distant. (B) Male-alone-distant. (C) Between the 7th and 20th min the male is on the nest; during the rest of the time the male is near the nest.

males were silent most of the time (55.1%) (Fig. 2). Males tend to sing continuously while on the nest and only fall silent toward the end of the incubation period or at the start of the nestling period.

The stimulatory influence of song from neighboring males is indicated by the small modal value for cadence in the context male–female-distant in Fig. 1. If a neighboring male is singing nearby, then the resident will engage in a song duel whether the female is present or not. The result is an increase in the number of cadences of short duration in the sample. However, all such effects could not be eliminated. It was obvious from field observations that male song activity decreased substantially or ceased in the following circumstance—when the male and female were together and not near the nest and when there were no other males singing nearby (see Fig. 3A).

Abandoned nests or mates.—In one pair the female disappeared late in the incubation period. Song output increased significantly (approx. $t = 8.585$, $P < 0.05$) from the 3 days prior to the disappearance (1.93 songs/min, N = 126 min) to the 3 days after (5.41 songs/min, N = 113).

The nests of two pairs were destroyed late in the incubation period; renesting did not take place. In both instances song output did not significantly change from the 3 days prior to nest destruction (2.35 songs/min, N = 133; 2.25 songs/min, N = 118) to the 3 days after (2.56 songs/min, N = 111; 2.03 songs/min, N = 120).

Bout structure.—There did not appear to be any consistent pattern in the delivery of song (i.e., bouts) among contexts. In male-pre-pair and male-alone-distant, birds tended to sing in bouts followed by intervals of silence of varying length (Fig. 3B). When near or on the nest, males sang almost continuously (Fig. 3C). In the context male–female-distant no obvious bouts were apparent (Fig. 3A).

Data on the bout structure of one male were gathered from all contexts and for the entire season. The mean number of songs per bout was 25.5 (N = 149 bouts), the mean bout length was 5.2 min (N = 148 bouts), and the mean interbout interval was 5.0 min (N = 134 intervals). The mean cycle length (the time from the beginning of one bout to the beginning of the next) was 10.2 min.

Changes related to the breeding season.—The song output (all contexts) of Warbling Vireos during the nest cycle is summarized in Table 2. Periods have been subdivided to show the changes in song output which occurred at the transition between periods. Durations of subdivisions were arbitrarily chosen or, in the case of shorter intervals, were chosen to increase individual sample size.

Most variation in song output during the season can be ascribed to two factors. The first relates to changes in context and the second to long term, likely physiological, changes. Since song activity changes with context, changes in song output during the season may reflect the time spent by birds in various activities. If a bird's physiology changes during the season, then it may be assumed that song output, irrespective of context, would also be affected to some degree. To help determine if this was occurring, song output was tabulated from one context (male-alone-distant) for the entire season (Table 2).

There was no significant difference ($t = 1.869$, $P < 0.10$) in overall song output from the pre-pair to the pre-nest-building period. In the pre-nest-building period mates spend on average 80.4% (N = 1245 min, N = 7 pairs) of their time together (within 10 m of each other). In this context male song activity was low (Table 1). Therefore, overall song output for the period would also be expected to decrease. It has often been reported in passerines that song activity of unmated males decreases substantially upon arrival of a mate (for reviews see Armstrong 1973, Catchpole 1982). However, it has not often been specified whether the effect is general or context dependent. The song rate recorded in the pre-pair period (male-alone-pre-pair, Table 2) was only slightly lower than the song rate of the comparable activity (i.e., patrolling the territory) in the pre-nest-building period (male-alone-distant, Table 2). The song rate was also calculated when the male was with the female during the pre-nest-building period

TABLE 2

MEAN SONG RATE AND STANDARD ERROR DURING THE BREEDING SEASON FOR ALL CONTEXTS AND FOR MALE-ALONE-DISTANT

Period	Sample interval (days)	Songs/min all contexts N[a] $\bar{x} \pm$ SE range $\bar{x}$[b]	Sample interval	Songs/min male-alone-distant N $\bar{x} \pm$ SE range $\bar{x}$
Pre-pair	entire	4 (49–101[c]) 3.10 ± 0.76 0.99–5.27	entire	—
Pre-nest-building	up to last 3 days	8 (26–325) 1.84 ± 0.30 0.33–3.10	entire	7 (34–66) 4.00 ± 0.28 3.11–4.94
	last 3 days	9 (63–118) 2.04 ± 0.41 0.19–4.66		
Nest-building	first 2 days	11 (60–245) 2.98 ± 0.23 1.70–4.24	first half	9 (23–120) 3.69 ± 0.30 2.01–5.30
	middle	12 (34–156) 2.90 ± 0.33 1.74–5.56	second half	10 (28–82) 4.62 ± 0.47 2.88–7.32
	last 2 days	12 (60–154) 2.78 ± 0.35 1.24–5.46		
Incubation	first 3 days	12 (100–265) 4.10 ± 0.52 1.42–7.03	first 3 days	8 (23–95) 5.33 ± 0.64 2.28–8.54
	middle	13 (206–641) 3.19 ± 0.34 1.31–6.02	middle	8 (69–242) 3.78 ± 0.24 1.49–6.26
	last 3 days	11 (66–180) 2.68 ± 0.32 0.98–4.71	last 3 days	9 (17–99) 2.95 ± 0.34 1.59–4.04
Nestling	first 3 days	11 (88–180) 1.99 ± 0.30 0.36–3.67	first 3 days	9 (13–88) 2.41 ± 0.40 0.38–4.11
	middle	11 (100–440) 2.31 ± 0.32 0.67–3.94	middle	9 (44–217) 2.12 ± 0.43 0.48–4.28
	last 3 days	11 (66–220) 1.90 ± 0.44 0.48–5.51	last 3 days	9 (46–133) 2.03 ± 0.56 0.11–5.77

TABLE 2
CONTINUED

Period	Sample interval (days)	Songs/min all contexts N[a] $\bar{x} \pm$ SE range $\bar{x}$[b]	Sample interval	Songs/min male-alone-distant N $\bar{x} \pm$ SE range $\bar{x}$
Fledgling	first week	11 (70–340) 1.99 ± 0.47 0.08–4.45	—	—
	to 4th week	6 (195–319) 1.29 ± 0.55 0–3.43	—	—

[a] N is individuals sampled.
[b] Range $\bar{x}$ is the range in means of individuals in songs/min.
[c] The range in total minutes recorded.

(1.43 songs/min, N = 9, samples for individuals ranged from 50–179 min) and was found to be significantly lower ($P < 0.01$) than the previous two contexts.

There occurred a significant increase ($P < 0.05$) in song output from the early pre-nest-building period to the first two days of the nest-building period. In part, an increase in song activity is expected in the nest-building period as males spend more time in contexts where they sing actively; 73.2% (N = 1538 min, N = 7 individuals) of the males' time was spent alone and away from the nest or near the nest. Song output decreased slightly during the nest-building period then increased during the first 3 days of the incubation period, however, differences were not significant (largest $t = 2.059$, $P > 0.10$). In the context male-alone-distant there occurred a significant increase ($P < 0.05$) in song rate between the first half of the nest-building period and the first 3 days of the incubation period. The increase was not associated with any obvious changes in the number or intensity of territorial interactions. The decrease in overall output during the nest-building period is likely due to changes in activity patterns. Males spend increasingly more time with the female during this period and, because the pair is away from the nest (26.9%, N = 1538 min) more than they are near it (9.1%, N = 1538 min), a decrease in male song output is to be expected. Song output at the beginning of the incubation period is high then because males spend all their time in contexts in which they sing actively (e.g., on the nest, patrolling the territory). At the beginning of the incubation period males tended to sing continually while on the nest.

There occurred a gradual and significant decrease ($P < 0.01$) in both overall song output and song output in the context male-alone-distant from the beginning of the incubation period to the end of the nestling period. The change in song rate was not attributable to any obvious change in the activity patterns of males, which remained relatively constant from day to day.

Breeding season and patterning of song.—To determine if a change in delivery of song occurred when the amount of singing changed, data on song activity were gathered when output was high (early incubation period) and low (early nestling period) for two contexts: male-alone-distant and male-on-the-nest (Table 3). A significant decrease ($P < 0.01$) occurred in both song and singing rates and a significant increase ($P < 0.05$) in the time spent silent from the early incubation period to the early nestling period for both contexts. The mean cadence values were not significantly different. The results may be due to differences in the continuity of song when the amount of singing changes. At low output levels song tends to be given in short bouts or sporadically. Song becomes less spontaneous and tends to be given only in response to specific stimuli such as during movements near the nest, at nest relief, and during interactions with neighboring males. At low output there occurs a greater number of minutes in which only one or two songs are recorded than when output is high. This would result in a lower singing rate, but would not necessarily affect cadence values.

Song activity and behavior.—During the nest-building period males spent 36% (N = 1538 min, N = 7 individuals) of their time accompanying their females to and from the nest. During this time the female gathers nesting material and constructs the nest. When the pair is together and away from the nest, the male is silent or sings infrequently. However, when approaching the nest the male sings at an increased rate and constantly. The effect of nest-centered song activity is apparent during courtship. A female mostly gives courtship vocalizations (see Methods) but also solicits by giving wing-quivers (for description see Barlow and Rice 1977), an apparent and immediate response to male song. However, this behavior by females is largely restricted to the vicinity of the nest (Howes-Jones 1982). Most courtship vocalizations (74%, N = 50) and wing-quivers (97%, N = 104) occurred within 10 m of the nest. Proximity to the nest appears necessary for female courtship behavior to be exhibited. Closeness to the nest seems especially important for the stimulation of wing-quivers. The female quivers her wings near the nest even when the male is not present or singing. Away from the nest pairs rarely engaged in courtship activity, however, when they approached the nest courtship activity commenced. Almost all copulatory attempts (48 of 50) were observed within 10 m of the nest.

TABLE 3

CHANGES IN SONG ACTIVITY WHEN SONG OUTPUT IS HIGH AND LOW

	Context			
	Male-alone-distant		Male-on-the-nest	
	Sample period		Sample period	
	Incubation	Nestling	Incubation	Nestling
Song Variables	N $\bar{x} \pm$ SE	N $\bar{x} \pm$ SE	N $\bar{x} \pm$ SE	N $\bar{x} \pm$ SE
Song rate (includes 0 songs/min)	10 5.08 ± 0.56	10*** 2.19 ± 0.41	10 3.20 ± 0.50	10*** 0.89 ± 0.24
Singing rate (excludes 0 songs/min)	10 6.08 ± 0.36	10*** 3.94 ± 0.30	10 3.64 ± 0.41	10** 2.00 ± 0.31
Time spent silent (%)	10 16.24 ± 7.12	10* 48.37 ± 8.84	10 16.49 ± 6.30	10*** 64.90 ± 8.03
Cadence (sec)	10 9.27 ± 0.40	10NS 10.37 ± 0.44	10 14.33 ± 1.00	9NS 14.76 ± 1.23

Statistical comparisons (*t*-test) are between periods for each context. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ NS = not significant.

During the incubation and nestling periods nest-centered song activity was evident during exchanges by adults involved in incubation, brooding, and feeding of young. In both periods males sang on 94.4% (N = 820) of their trips to the nest and on 65.1% (N = 690) of their departures from the nest. When a male approaches the nest his song appears to be a cue to the female to fly from the nest. Near the end of the incubation period some males sang only when flying to the nest. In response, the female almost always flew off the nest.

All male Warbling Vireos which I observed sang while sitting on the nest. The regular and moderately paced song given by incubating or brooding males is distinctive and to the experienced observer indicates the bird's activity. Generally, when the male is on the nest the female initiates an exchange of positions by approaching the nest and calling. At this point the male flies off the nest. Less often the male may initiate an exchange of position. Two methods are used. In the first case the male flies off the nest when the female is absent and silent. After a short delay the female flies to the nest. In the second case, if a male has been sitting on the nest for a long period he may start to sing faster, at which point the previously distant female may then fly to the nest. Males sitting on the nest sometimes increase the tempo of song in response to an approaching female.

DISCUSSION

Smith (1977) suggests that animals maximize their limited 'message space' by using contextual sources of information which increase the functional breadth or range of the signal. In the Warbling Vireo, song rate, cadence, and output changed with the proximity of the male to the nest, to the female, and with the stage of the breeding season. Changes in song activity appear to function in a variety of ways to help integrate the social activities of the pair.

During the nest-building period nest-centered singing appears important in the integration of sexual activities. Both proximity to the nest and male song appear necessary to evoke courtship behavior by the female. If both factors are important, then nest-centered song is advantageous because it promotes maximal stimulation of the female in a locale where she is already primed for activity. In this context, song likely exerts a tonic or priming effect on the female (Schleidt 1973, Smith 1977:234). Reduction in singing, which occurs when the pair is together and away from the nest, is also advantageous because it minimizes stimulation of the female in an area where copulation is not likely to occur and also may reduce interference from neighboring males.

One of the functions accredited to passerine song as a courtship signal is in the sexual stimulation of the female and the synchronization of courtship behavior (Brockway 1965, 1969; Armstrong 1973:156–160; Hinde and Steel 1976; Kroodsma 1976; Miller 1979). The role that the amount of song plays in courtship in *V. gilvus* is not clear. In many passerines song output peaks several days before egg-laying at a time corresponding to ovulation (Catchpole 1973, 1982; Slagsvold 1977). However, this relationship may not be a general one, as Armstrong (1973) lists many species in which peak singing does not coincide with a time several days before egg-laying. In the Warbling Vireo song output peaked at the start of the incubation period. Although total song output (all contexts) is likely important in the stimulation of the female, it is possible that singing in the appropriate context is also important. A continuous and high rate of song near the nest during the nest-building period is likely the important factor in the Warbling Vireo. Brockway (1969) found in Budgerigars (*Melopsittacus undulatus*) that only a certain quantity of the appropriate vocal stimuli was important in stimulating the female and that a further increase in quantity had no effect.

At the start of incubation, nest-centered song acquired the different function of coordinating movements of the pair to and from the nest. The giving of song on approaches to the nest signals the male's presence and probable intention to sit on eggs and acts as a cue for the female to

fly off the nest. In this context, song activity has a more discreet effect or is informative (Schleidt 1973, Smith 1977:234).

Singing by male Warbling Vireos on the nest has been noted by others (Miller 1902, Rust 1920, Sutton 1949, Bent 1950). The contrast in cadence, rate, and direction of song, which occurs when the male is on then flies off the nest, allows the female to ascertain when the male is on the nest and when she should fly to the nest. Warbling Vireos can and do use a variety of call notes to maintain contact and synchronize movements at the nest (Howes-Jones 1982), which suggests that there might be other reasons why males sing on the nest. Singing from the nest may be tied to the fact that Warbling Vireos are prodigious singers and have complex songs (Hartshorne 1956, Howes-Jones 1982). A cessation of song on the nest would create a regular and obvious on-off pattern in song activity which might alert potential nest predators. Regular vocal contact is essential to the relationship between mates (Howes-Jones 1982). Consistency in the output of song may also be tied to the maintenance of the territory.

Reduction of song during pair formation is characteristic of many passerines and has often been used as evidence to indicate that active singing attracts females (Armstrong 1973:152, Catchpole 1982). In the Warbling Vireo the reduction in overall song output at pairing was due mostly to a change in activity patterns (i.e., female presence seemingly causes a reduction in male song). The song rate in the pre-pair period was slightly lower than the song rate in the comparable context (male-alone-distant) in the pre-nest-building period. This difference does not preclude the fact that a high song rate may attract females. It does indicate that the effect of female presence on song activity is context specific. That a high rate and output of song may attract mates is also indicated by the observation that the song output of a male whose female disappeared during the incubation period increased substantially. For two males that remained mated after their nests were destroyed, however, song output remained unchanged. When the male and female are together prior to nest-building, song activity is unique (variable cadence, sporadic output, large amount of time spent silent) and as such may convey that the male has a mate.

In this study part of the variation in song output during the season was ascribed to changes in the activity patterns of birds. The fact that song activity can change with context suggests that any interpretation of general or seasonal changes in song output requires the examination of both context related factors and changes in activity patterns. A decline in singing during incubation is typical of other birds and has generally been ascribed to a reduction of androgen levels and to the appearance of the

young (Davis 1958, Lehrman 1959, Andrew 1969, Lofts and Murton 1975, Nottebohm 1975).

Differences in cadence among species have been described (Reynard 1963), however, changes in cadence among contexts within a species are not well understood. In other passerines cadence has been found to increase when males sang with neighbors (Heckenlively 1976), to be regular, or to increase with a decrease in output (Davis 1958). The relevance of the patterning of songs over an extended period of time (i.e., bouts) has also received scant attention (for exception see Thompson 1972). The general problem of temporal patterning in song, its relationship to context, and encoded message requires further research.

ACKNOWLEDGMENTS

I am grateful to W. Thompson for his comments and suggestions about this manuscript. Funds in support of this research, which in part encompasses data gathered during doctoral research at the University of Toronto by Howes-Jones, was provided by grant A-3472 to J. C. Barlow from the Natural Science and Engineering Research Council of Canada.

SUMMARY

The song activity of Warbling Vireos (*Vireo gilvus*) in southern Ontario was quantified using the variables of song rate, cadence, and time spent silent. Song activity changed substantially with context (six defined) and with season. Contexts were defined in terms of the proximity of the male to the female and to the nest. In the immediate proximity of females, males are silent or sing sporadically except when engaged in a song duel with another male or when near the nest. In close proximity to the nest, song tends to be continuous and has a short cadence. Song delivered on the nest has a long and regular cadence. Males appear to sing in bouts only when they are alone, away from the nest, and are patrolling their territories. In part, changes in song output with different stages of the breeding cycle were due to changes in activity patterns as the result of the context dependency of song rate and output. Gradual changes in song activity occurred during the breeding cycle. Changes in song activity were related to: establishing contact with a potential mate; integrating courtship behavior so that it occurs only in the vicinity of the nest; as a means for monitoring a bird's activity and location; and in coordinating movements of birds to and from the nest.

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ERRATA

In D. A. Boag's review of "The grouse of the world" by P. A. Johnsgard (Wilson Bull. 96:337–338, 1984), the genus name of *Dendragapus* is misspelled on page 338. Also, the penultimate sentence should read ". . . the Spruce and Sharp-winged grouse closer to the Blue Grouse . . . ."

Wilson Bull., 97(1), 1985, pp. 21–29

DEVELOPMENT AND USE OF TWO SONG FORMS BY THE EASTERN PHOEBE

Donald E. Kroodsma

Vocal development among oscines typically involves some form of vocal imitation, with young birds learning the songs of adult conspecifics or heterospecifics during early life (e.g., Slater 1983). In the field, the consequences of this vocal learning are readily apparent in the form of local song traditions (Mundinger 1982) or interspecific mimicry (Baylis 1982). In the laboratory, juvenile oscines denied experience with conspecific song typically develop very abnormal songs or else learn the songs of other species (Kroodsma 1982).

Vocal development may be very different in the more "primitive" passerine suborder, the suboscines. In a study of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*), I could find no difference between the songs of wild birds and the songs of males or testosterone-treated females that were hand-reared in the laboratory from seven to ten days of age and denied access to conspecific song models (Kroodsma 1984). Vocal learning appears to play a negligible role in song development in these two *Empidonax* species. Such an interpretation is consistent with the relative absence of geographic vocal variation found in this genus (Stein 1963, Payne and Budde 1979, Johnson 1980).

Together with morphological characters such as sperm structure, stapes structure, and syrinx complexity (e.g., Feduccia 1980), the mode of vocal development may distinguish the oscines from the suboscines. However, more data on vocal ontogeny are needed from other suboscines before such a generalization can be accepted confidently. I therefore initiated a study of vocal development in the Eastern Phoebe (*Sayornis phoebe*), a species closely related to the *Empidonax* complex (W. E. Lanyon, unpubl. data). Here I report that male and female laboratory-reared phoebes not only develop the two song forms characteristic of the species (Smith 1977) but that they also use them in typical wild-type fashion.

METHODS

On 20 June 1981 I collected five Eastern Phoebe nestlings from a nest in Amherst, Massachusetts; the eyes of the nestlings were closed, and the birds fledged 10 days later, on 30 June. I estimated the nestlings were about five to six days old when collected. Birds were maintained on a daylength consistent with 42°N latitude.

In the laboratory these birds heard the songs of Willow Flycatchers and Marsh Wrens (*Cistothorus palustris*) over loudspeakers, but no songs of phoebes. The five birds were housed in separate cages but in the same room until early spring, when each bird was placed

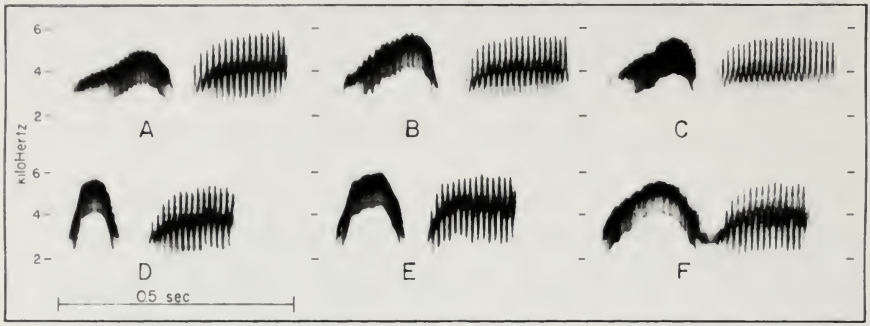

FIG. 1. The *fee-bee* song form of the Eastern Phoebe. Birds A and B are wild birds recorded in New York (LNS Catalogue Nos. 7913, 7917, respectively), and Bird C is from Massachusetts (Recording 5-308 in DEK library). Birds D, E, and F are hand-reared birds. Bird E is a female with a testosterone implant; D and F are males.

in a sound isolation chamber until it came into full song. The three males sang frequently. Smith (1977) has heard wild females sing, but I heard the two laboratory-reared females sing only after a 15-mm section of silastic medical tubing packed with crystalline testosterone was placed beneath the skin.

Several recordings were obtained from the Cornell Laboratory of Ornithology (Library of Natural Sounds [LNS] Cuts 7911–7919, 19782), and I recorded several adult phoebes in the vicinity of Amherst, Massachusetts. Field recording equipment consisted of a Nagra IS-DT or IV-S and either a Sennheiser 816 shotgun microphone or a Sennheiser 104 mounted in a 24 in. parabolic reflector. Tape speed was either 3¾ or 7½ ips. Sound spectrograms were prepared on a Kay Elemetrics Co. 7029A Sona-Graph (wide-band setting).

RESULTS

Song forms of wild and laboratory-reared adults.—As described by Smith (1969, 1977), each adult phoebe regularly sings two different song forms (Figs. 1, 2). The one used most frequently sounds like *fee-bee,* and gives the bird its name. The second song form begins in the same way, but the bird seems to stutter on the second half of the song; Smith renders this song *fee-b-be-bee,* though the *bee*'s of the two song forms are quite different.

The *fee-bee* songs of different individuals are usually distinguishable after fine scrutiny of sonagrams. For example, the songs of Birds A, B, and C in Fig. 1 have frequency modulations in the *bee* at the rate of 10 per 0.128, 0.120, and 0.117 sec, respectively, and the rate is highly stereotyped within a male (e.g., 10 consecutive songs from Bird C gave a mean of 0.117 sec, SE = 0.00007 sec, CV = 1.91%).

The five hand-reared birds, including three males and two females, all developed very typical *fee-bee* songs (Fig. 1). I measured the overall duration of the song, the duration of the *bee* portion, the number and rate

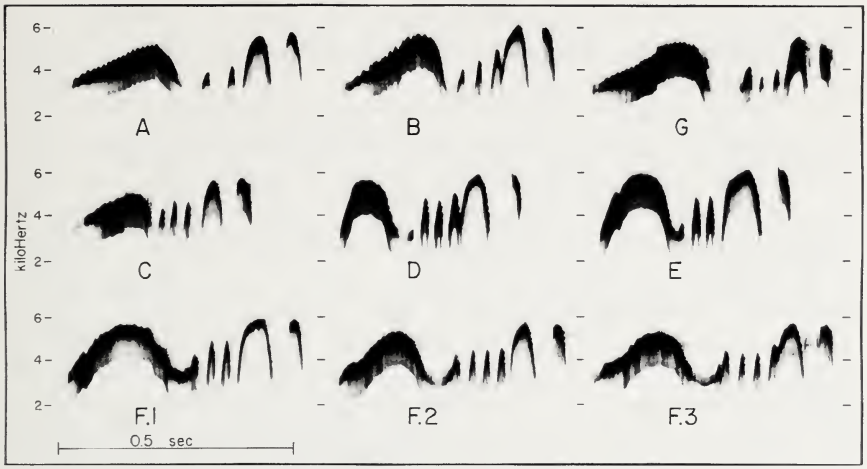

FIG. 2. The *fee-b-be-bee* song form of the Eastern Phoebe. See Fig. 1 legend for identification of Birds A–F; Bird G is an adult male from North Carolina (LNS Cat. No. 7915). Three song forms (F.1, F.2, F.3) are displayed for Bird F.

of frequency modulations in the *bee,* and the maximum frequency of both the *fee* and the *bee*; I could find no significant differences when these parameters were compared to measured parameters in the songs of five wild individuals.

The *fee-b-be-bee* songs appear more variable among males. The *b-be-bee* portion consists of varying numbers of notes with different temporal organizations (Fig. 2), yet each male sings a highly stereotyped form of this song. It is possible that there is geographic variation in these parameters, yet four males from Ithaca, New York (LNS Cat. Nos. 7913 [Bird A], 7917 [Bird B], 7911, and 7914) displayed nearly the full spectrum of variation seen in wild birds. Furthermore, during song development, Bird F (Fig. 2) also sang several variations, indicating that each individual is capable of producing several renditions of this song. Apparently most wild males settle on one particular variation, but I had not recorded Bird F long enough in the laboratory to obtain that stereotypy. As with the *fee-bee* song, I could find no consistent differences between the songs of laboratory-reared birds and wild birds.

Singing behavior of adult males.—Smith (1969, 1977) noted that the proportion of the two song forms during a given performance varied with the rate of singing. In order to assess this feature in both the wild and laboratory-reared males, I determined the proportion of *fee-bee* songs during 1-min samples from dawn singing sessions.

In all five males, two from the laboratory and three from the wild, the

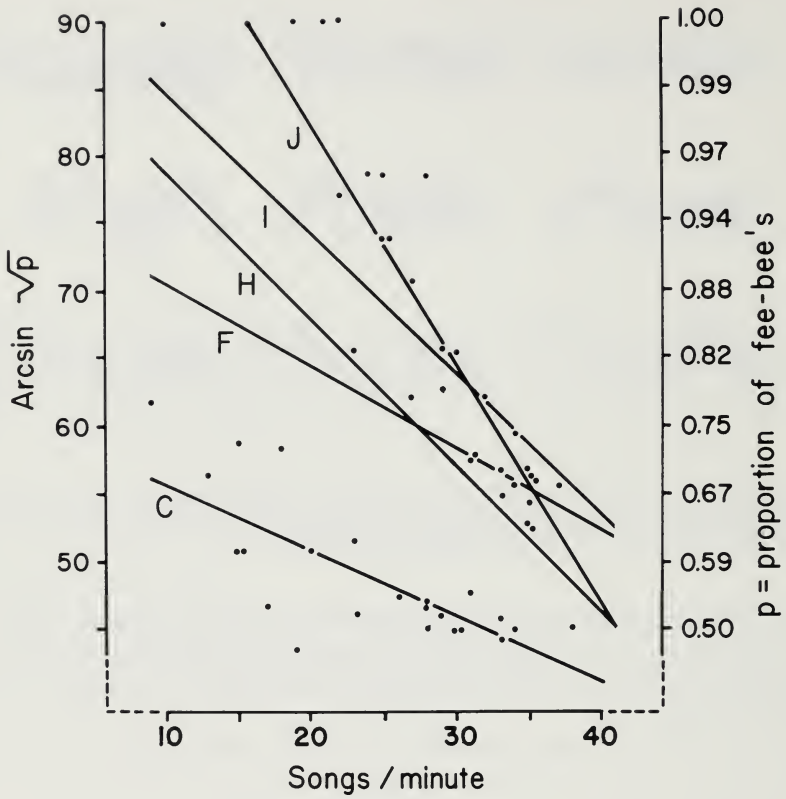

FIG. 3. The relationship between the rate of singing in songs per min and the proportion of *fee-bee* songs in a singing performance. The proportion and its angular transformation (arcsin $\sqrt{p}$) are both given on the abscissa; calculations are performed with the transformed values. Birds F and H are hand-reared laboratory males; Birds C, I, and J are wild males recorded in the Amherst area between 19 May and 1 June 1984 (DEK Recordings 5-308, 5-307, and 5-306, respectively). Songs of Birds C and F are displayed in Figs. 1 and 2. The regression coefficients, slope, and number of 1-min sample periods, respectively, are as follows: C (−0.76, −0.50, 23), F (−0.72, −0.59, 30), H (−0.84, −1.08, 30), I (−0.88, −1.04, 18), J (−0.90, −1.80, 30). To illustrate the variation in the data, I have displayed the data points for Birds C and J; all data points above line H are for Bird J, all data points below for Bird C. All five regression analyses are highly significant at $P < 0.001$.

rate of singing and the proportion of *fee-bee* songs in the performance were inversely related ($P < 0.001$, Fig. 3). Males clearly differed from one another. When Bird J, for example, sang fewer than 25 songs per min, nine out of ten 1-min sample periods consisted of more than 90% *fee-bee*'s. Bird C, on the other hand, never sang more than 80% *fee-bee*'s,

even though his rate of singing dropped as low as 10 songs per min. The singing of the two laboratory males was comparable to that of the three wild males.

One other intriguing feature of Eastern Phoebe singing behavior involves the temporal relationship of the two song forms during a singing performance (see Table 1). During early morning singing, there is a relatively short pause between the delivery of a *fee-bee* and a *fee-b-be-bee* song form (median value from beginning of first song to the beginning of the second song for five males = 1.65 sec; sample sizes for each male are given in Table 1), a slightly longer pause between successive *fee-bee*'s (1.81 sec), and the longest pause between the *fee-b-be-bee* and the next *fee-bee* (2.06 sec); successive *fee-b-be-bee*'s rarely occur. Except for Bird C, where a small sample for *fee-bee* to *fee-bee* transitions probably does not represent the actual distribution, this pattern held for all birds, and the laboratory and wild birds did not differ in their behavior. Furthermore, not only is the time from the *fee-bee* to the *fee-b-be-bee* much briefer, but it is also much less variable, as indicated by the coefficients of variation (CV). For the four males with sufficient sample sizes ($N > 20$ for all three transitions), the median CV for each of the three transitions was 9.1, 22.6, and 23.0, respectively.

The rate of singing increases as the proportion of *fee-b-be-bee* songs increases. However, because of the characteristic temporal relationships of the song forms, the sequence from *fee-bee* to *fee-b-be-bee* to *fee-bee* (3.22, 4.24, 3.71, and 3.69 sec for Birds F, H, I, and J, respectively) actually takes about as long as it does to go from *fee-bee* to *fee-bee* to *fee-bee* (3.38, 4.34, 3.62, and 3.40 sec for Birds F, H, I, and J, respectively). Thus, the relationship between the rate of singing and proportion of the two song types in the performance is not simply explained by the relative time for transitions between different song types. Neither does the duration of the two song forms explain this relationship. In two males (F and H) the duration of the *fee-bee* was greater than the *fee-b-be-bee* while it was just the reverse for Bird J; the two song forms were the same length for the fourth bird (I).

DISCUSSION

The song forms and singing behavior of five Eastern Phoebes, hand-reared in the laboratory and isolated from conspecific songs from about five or six days of age, appear very similar to the songs and behavior of wild males. The sonagrams are indistinguishable from wild-type songs, and the hand-reared birds during early morning singing produced not only the typical inverse relationship between the rate of singing and proportion of *fee-bee*'s but also the typical temporal distribution of the two song forms.

TABLE 1

TEMPORAL ORGANIZATION OF SINGING BEHAVIOR IN TWO LABORATORY (F, H) AND THREE WILD (C, I, J) ADULT MALE EASTERN PHOEBES

Bird	Song transition $\bar{x}$ (sec) ± SE			Duration of songs[a]
	fee-bee to *fee-b-be-bee*	*fee-bee* to *fee-bee*	*fee-b-be-bee* to *fee-bee*	*fee-bee*/*fee-b-be-bee*
F	1.39 ± 0.03 (N = 22, CV = 9.2)	1.69 ± 0.05 (N = 29, CV = 16.7)	1.83 ± 0.06 (N = 22, CV = 15.7)	0.43/0.49
H	1.71 ± 0.03 (N = 62, CV = 12.0)	2.17 ± 0.07 (N = 144, CV = 37.2)	2.53 ± 0.14 (N = 65, CV = 45.1)	0.48/0.52
C	1.86 ± 0.09 (N = 89, CV = 47.5)	3.45 ± 0.46 (N = 7, CV = 35.2)	2.43 ± 0.14 (N = 89, CV = 52.6)	0.49/0.39
I	1.65 ± 0.02 (N = 25, CV = 6.4)	1.81 ± 0.08 (N = 25, CV = 23.4)	2.06 ± 0.05 (N = 25, CV = 12.6)	0.50/0.50
J	1.53 ± 0.03 (N = 25, CV = 9.0)	1.70 ± 0.07 (N = 25, CV = 21.7)	2.16 ± 0.13 (N = 25, CV = 30.2)	0.50/0.42

[a] Average of two to 10 songs for each male.

The apparent lack of vocal imitation during ontogeny is similar to that found in the Alder and Willow flycatchers (Kroodsma 1984), and all three flycatcher species contrast sharply with vocal development typical in oscines. Songbirds reared in isolation from conspecific song would typically develop either highly abnormal song or learn songs of heterospecifics (e.g., Lanyon 1957, 1979; Marler 1970; Ewert 1979).

Songbirds actually have two "critical periods" during song development (Nottebohm 1969, Marler and Peters 1982). During the first phase, songs of other adults are memorized; during the second phase, the young bird attempts to match its motor output with this model stored in the brain. In some species these two phases overlap, but in others they may not. The three flycatcher species that I have studied lack the first critical period, for young birds do not have to imitate songs of other adults in order to produce normal songs. Thus, the song "template" (Marler 1976) is not refined by vocal learning.

It is unclear whether these flycatchers have a developmental phase analogous to the second learning phase of songbirds. Fledgling flycatchers use calls that are rudimentary forms of the adult songs, and it is possible that the motor output is gradually perfected by comparing the vocal output with an innate song template. Determining whether or not these flycatchers are *learning* to match the motor output of the syrinx with an inherited song template will require experimental work with deafened suboscines (Konishi and Nottebohm 1969, Nottebohm 1975).

The variation in the *fee-b-be-bee* song form produced by Bird F does suggest the possibility of one form of environmental influence on vocal development. This male appears capable of producing a variety of these song forms, but it is possible that the one favored is that which matches the singing of other adults in the vicinity. This might be tested by looking for "neighborhood effects" (i.e., dialects) in the field or by rearing nonrelated males together in the laboratory to determine whether they converge on similar song forms. Thus, a subtle form of vocal learning could influence the details of the final song form, but learning from other phoebes is not necessary for the development of wild-type song forms and behavior.

The data reported here further support the possibility of a distinct difference in vocal development between the suboscines and the oscines. I have now examined three flycatcher species from the Tyrannidae, and have found that vocal development proceeds normally in nestlings isolated from conspecific song. There are, of course, another 1094 suboscines (Bock and Farrand 1980), including pittas, ovenbirds, antbirds, cotingas, as well as other tyrannid flycatchers, some of which have more compli-

cated songs and singing behaviors than the Eastern Phoebe, Alder Flycatcher, and Willow Flycatcher. Careful study of vocal development in some of these species would be especially welcome in attempting to sketch the evolution of vocal learning in the order Passeriformes.

SUMMARY

Five Eastern Phoebe (*Sayornis phoebe*) nestlings were collected at five to six days of age and reared in the laboratory. The three males and two females heard heterospecific but no conspecific song, yet each developed the two wild-type Eastern Phoebe song forms (*fee-bee,* Fig. 1; *fee-b-be-bee,* Fig. 2) and used the two song forms normally during early morning singing performances (Fig. 3, Table 1). These data are consistent with the hypothesis that vocal development among the suboscines requires no imitation of conspecifics. This is in sharp contrast to the oscines, the more "advanced" passerine suborder, where vocal learning is the rule.

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STRUCTURE AND VARIABILITY IN THE VOCAL REPERTOIRE OF THE MOUNTAIN CHICKADEE

PHILIP K. GADDIS

The vocalizations of North American chickadees (*Parus*, subgenus *Poecile*) are diverse and complex. The complete vocal repertoires of a few species have been described and illustrated with sound spectrograms (Smith 1972, McLaren 1976, Ficken et al. 1978) and various other vocalizations from other species have been discussed (e.g., Sibley 1955, Dixon et al. 1970). These works indicate a great deal of variability in the chickadees' vocalizations, but, except for songs, no attempts have been made to analyze their patterns of variability quantitatively. As a first step toward an understanding of the communicative significance of this variability, I attempt in this paper to characterize the patterns of variability of different vocalization categories in the repertoire of the Mountain Chickadee (*Parus gambeli*). Comparisons are then made with existing information on the vocalizations of other chickadee species in an attempt to define general patterns of repertoire organization in these birds.

METHODS

The vocalizations of Mountain Chickadees were tape recorded between February 1980 and February 1981. The majority of the recordings were collected between February and May 1980 and between November 1980 and February 1981. The primary study area was located just north of Flagstaff, Coconino Co., Arizona, in second growth forest of ponderosa pine (*Pinus ponderosa*) and Gambel oak (*Quercus gambelī*) at an elevation of 2200 m. Recordings were also made at five other sites (elevation 2130–2740 m) located 2–10 km from the primary study area.

Recordings were made with a Uher 4400 recorder with a Dan Gibson parabolic reflector microphone and also on a Superscope CD330 cassette recorder with a Bell and Howell directional condensor microphone. Tapes were analyzed on a Kay Elemetrics 6061B Sona-Graph using 80–800 Hz, wide-band, linear display modes. The resulting spectrograms were sorted into categories based on structural similarity.

Two techniques were used for evaluating the thoroughness of sampling of the various call categories and measured characters. Completeness of sampling was determined by plotting the cumulative repertoire size (number of distinctive states for the parameter being considered) as a function of call number. In order to overcome artifacts arising from possible nonrandom selection of call forms during bouts of calling, all of the calls to be considered were pooled and drawn randomly. The cumulative repertoire size was then plotted against the number of calls considered to that point. The resulting plot tends to level off as the limit of all possible states is approached asymptotically.

A similar technique was used to evaluate the extent to which the variability of a continuously varying parameter was characterized by the sample. Instead of repertoire size, the standard deviation (SD) at every 5th or 10th datum (for $N > 200$) was plotted as a function

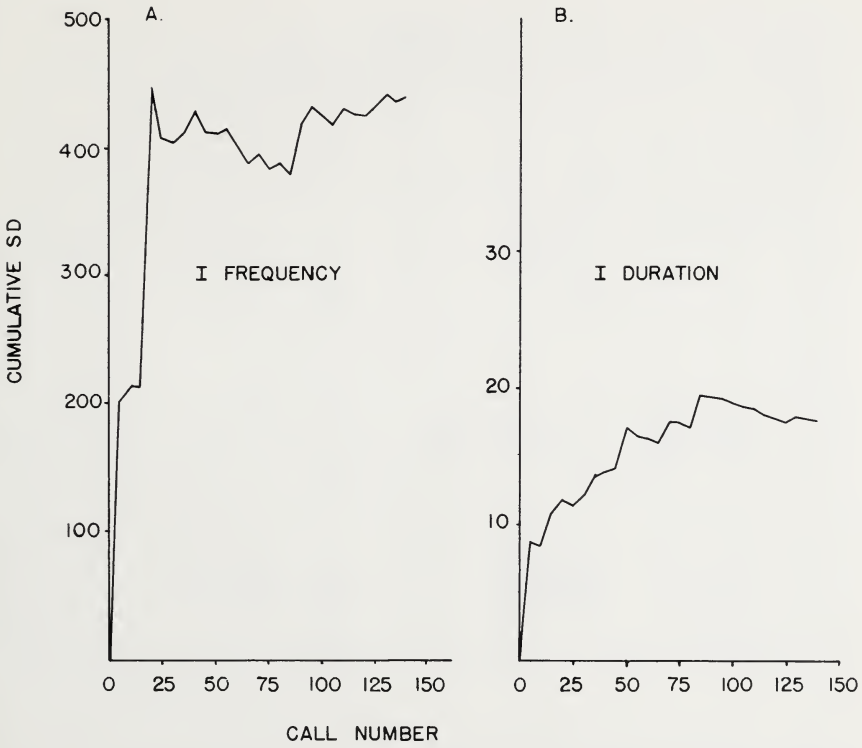

FIG. 1. Cumulative standard deviation of category I element frequency (A) and duration (B).

of randomized datum number. These plots rise steeply at first, then asymptotically approach the true value for the population (two representative examples are shown in Fig. 1). The magnitude of the fluctuations can be taken as an indicator of sampling completeness and expressed in two ways. First, the extent of SD fluctuation (maximum SD − minimum SD) in the final 50%, 25%, and 12.5% of the randomized data sequence was expressed as percentages of the final SD. Second, the 95% confidence interval of the variance was calculated (Sokal and Rohlf 1969, p. 154) and accommodated to the SD plot. The magnitude of fluctuations in the final 25% of the randomized data sequence was expressed as the percentage of the 95% confidence interval.

These calculations were intended to broaden the basis for assessing sampling thoroughness and the variability of various measures. They will also provide a means of comparing the variability of comparable vocalization characteristics of other species when suitable data become available.

Levene's test (Van Valen 1978) was used to compare the variability of characters with different distributions. In this test, deviations from the mean were compared for the two distributions in a one-way analysis of variance.

Behavioral correlates of category II calls were analyzed using a Chi-square contingency

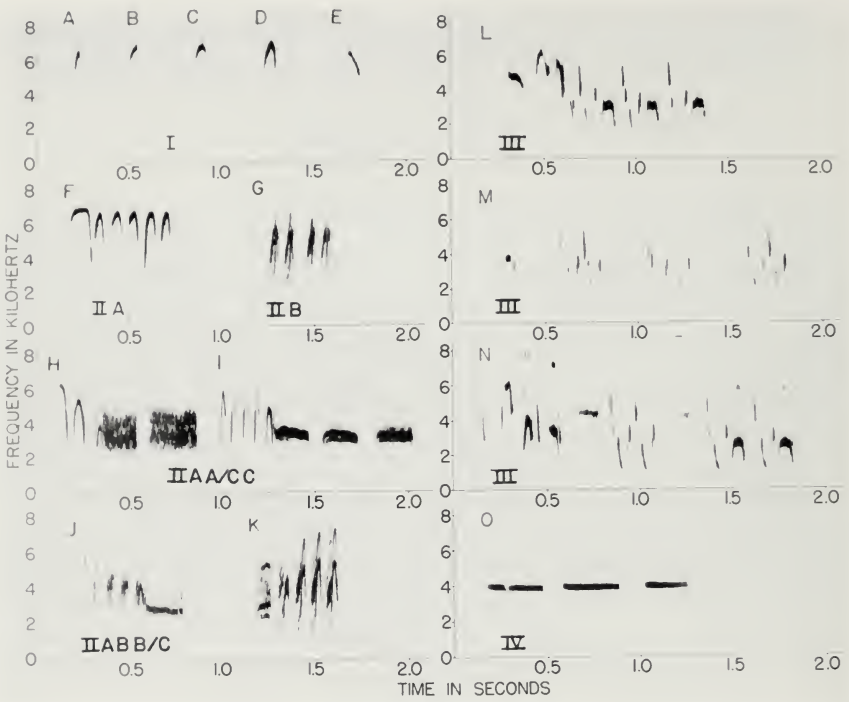

FIG. 2. Overview of the vocal repertoire of the Mountain Chickadee. A–E, representative examples of short-range contact calls, category I; F, series of IIA elements; G, series of IIB elements; H and I, two series containing IIA elements, a fused IIA/C element, and IIC elements; J, series containing two IIA elements, two IIB elements, and a fused IIB/C element; K, series given by a female during courtship begging; L–N, calls of category III—L, A_1–B_1–B_1–B_1; M, A_2–B_2–B_1–B_1, lower harmonics of the high frequency elements appear before and after the B_2 phrase; O, whistled song category IV.

table. Occurrence frequencies were considered large enough for statistical testing if the expected frequency for each cell was larger than one (Snedecor and Cochran 1967).

RESULTS

Three hundred and fifty-nine calls were analyzed spectrographically. Extensive variation was found in the acoustic structure of these calls, but they were separable into four general categories on the basis of a few simple criteria. That these were natural categories was confirmed by the apparent separation into usage categories (see below). The four categories were: I, single, arch-shaped elements; II, multi-element series consisting of elements from any of three types in a characteristic order (the "*chick-ka-dee-dee*" call); III, fast, sputtery calls consisting of rearrangeable phras-

TABLE 1
FREQUENCY (HZ) AND DURATION (MSEC) OF CATEGORY I AND II ELEMENT TYPES

	N	$\bar{x}$	±SD	CV	% ΔSD^{50}	% ΔSD^{75}	% $\Delta SD^{87.5}$	ΔSD as % of 95% confidence interval
I frequency (Hz)	139	6857	±440.8	6.4	14.9	5.9	2.1	23.6
I duration (msec)	139	58.6	±18.0	30.7	13.4	5.8	1.8	24.5
IIA frequency	248	6758	±542.5	8.0	10.1	2.4	1.8	10.1
IIA duration	248	62.7	±20.9	33.4	3.0	3.0	2.2	18.1
IIA^1 frequency[a]	83	7101	±540.5	6.7	8.9	3.3	3.3	10.3
IIA^1 duration	83	81.3	±19.6	24.1	15.5	4.3	1.2	13.5
$IIA^{A/C}$ frequency[b]	80	5237	±324.8	6.2	3.6	3.6	0.7	11.1
$IIA^{A/C}$ duration	80	43.9	±10.2	23.3	11.6	3.9	3.9	11.8
IIA–IIA ied[c]	120	37.3	±5.4	14.3	10.3	5.9	2.9	21.3
IIA–$IIA^{A/C}$ ied	65	56.5	±22.3	39.5	19.9	4.7	4.7	12.9
IIA/C duration	70	191.2	±30.0	15.7	30.7	1.8	1.8	5.4
IIA/C–IIC ied	33	70.1	±15.8	22.5	—	—	—	—
IIB duration	115	40.1	±5.9	14.8	14.3	13.0	6.5	39.9
IIB–IIB ied	90	60.4	±24.0	39.7	11.5	9.8	9.8	34.2
$IIC^{A/C}$ duration	76	134.0	±31.9	23.8	21.6	3.5	3.5	10.7
IIC duration	130	249.8	±35.0	14.0	8.9	2.5	1.8	16.3
IIC–IIC ied	32	76.5	±19.2	25.1	—	—	—	—

[a] IIA^1 = first IIA element of series.
[b] $IIA^{A/C}$ = IIA portion of fused A/C element.
[c] ied = inter-element duration.

es; and IV, series of long whistle-like elements. These were not entirely discrete categories; intermediate calls containing features of two categories were occasionally expressed. These intermediates, however, were rare, and the great majority of calls fell clearly into one of the four categories.

Category I.—Calls of category I consisted of a single arch-shaped element, which varied in frequency, duration, and in the details of shape (Fig. 2A–E). Table 1 and Fig. 1 indicate that the sample is sufficient to represent the true variability of the measured parameters. There was no correlation between frequency and duration of category I elements ($r = 0.04$, $P > 0.05$).

Category I calls were given during virtually all observed activities and could be mixed with all other kinds of calls, but they were the predominant calls for long periods, during slow and even flock movements as the birds foraged. The chickadees tended to forage discontinuously, spending 30–60 sec in a given tree or ground patch and giving three–five calls there before flying to another patch.

Category II.—Calls of category II consisted of series of several elements

TABLE 2

CATEGORY II CALL STRUCTURE IN TERMS OF ELEMENTS/SERIES OVERALL AND ELEMENTS/SERIES OF THE DIFFERENT ELEMENT TYPES

	N	$\bar{x}$	±SD	CV
Elements/series	129	5.3	±2.0	37.8
IIA elements/series	110	2.5	±1.2	47.6
IIB elements/series	29	3.9	±2.0	50.4
IIC elements/series	81	1.7	±0.7	42.9
IIA/C elements/series	87	1.0	±0.0	—

drawn from three basic types (Fig. 2F–I). Although graded intermediates were possible between types, these were unusual and type divisions within call series were usually discrete. Call elements of type B were distinguished from those of type A by the presence of additional, higher frequency components in the ascending portion of the arch. Call elements of type C consisted of relatively long duration, broad-spectrum elements that occasionally showed the evenly banded structure indicative of harmonics. Series usually contained a fused A/C element (Fig. 2H,I), and a few fused B/C elements were also recorded (Fig. 2J). The fluctuations of all SD plots were within the final 95% confidence interval through the second half of the randomized data points (Table 1). Temporal variation was consistently greater than frequency variation.

Within a given series the arrangement of element types, with rare exceptions, followed the pattern A before B before C. Series could contain one to several elements of any of these types, but elements were segregated according to type. Fused A/C elements, when present, occurred between A and C elements and never in the same series with a B element. The series averaged 5.3 elements per series with a strong mode (31% of the sample) of four elements per series (Table 2, Fig. 3).

Although the composition of category II calls was restricted by these patterns of element arrangement, there nevertheless remained considerable freedom for the expression of a great diversity of arrangements (Fig. 4). The majority (70%) of forms occurred only once. Many other arrangements are conceivable, and it appears likely that continued sampling would result in an extended repertoire. Furthermore, the variability in frequency and duration of the elements afforded this species a potentially enormous repertoire of calls in this category.

Type A elements varied considerably within a given series, but not without definable pattern. These elements invariably descended in frequency within a series (Table 3) and, at the same time, became shorter

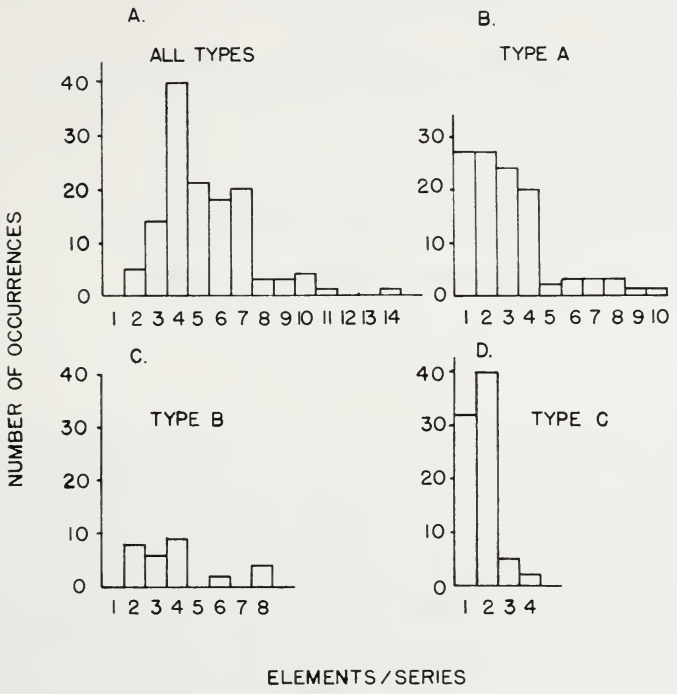

FIG. 3. Occurrence frequency histograms for category II elements/series; A, all element types considered together; B, elements of type IIA; C, elements of type IIB; D, elements of type C.

in duration (linear regression of frequency against duration: $r = 0.66$, $P < 0.01$). No such patterns were found in the variability of type B or C elements.

Linear regression of inter-element duration against the duration of the preceding element showed a significant correlation for only one of five element types, the C–C interval ($r = 0.51$, $P < 0.001$). Intervals between A elements, between A and A/C, A/C and C, and between B elements showed no such relationship (intervals between A and B, and between B and C were too rare for testing). This suggests that cadence (i.e., even rhythmicity) was an important feature only in series of C elements. Furthermore, only in the case of C series is there an indication that onset to onset duration (the beginning of one element to the beginning of the next) is conserved. This is indicated by a lower coefficient of variation for onset to onset duration (7.1) than for element duration (14.0) (Levene's test, $F = 13.12$, df = 1, $P < 0.01$).

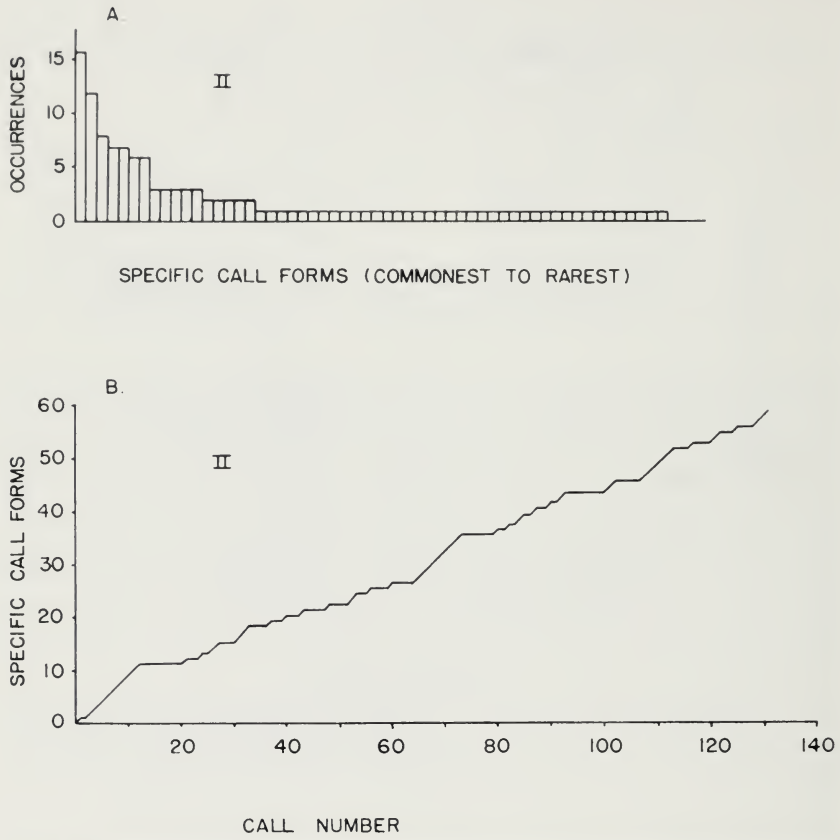

FIG. 4. A, occurrence frequency histograms for specific call forms of category II, arranged in order of abundance in the recorded sample from commonest to rarest; B, cumulative repertoire size for specific call forms of category II.

Chickadees rarely, if ever, repeated a given call form identically in every detail, but forms given in the same bout usually showed common features. This tendency was evaluated for several bouts by an analysis of variance of three parameters, all of which showed significantly greater between bout variation than within. These parameters were: elements/series ($F = 26.2$; df = 3,41; $P < 0.001$), frequency of first A element ($F = 42.3$; df = 5,41; $P < 0.001$), and duration of C elements ($F = 43.7$; df = 4,64; $P < 0.001$).

Calls of category II were typically associated with changes in the movement patterns of the callers or of the entire flocks of up to eight individuals. The calls were usually answered by others and occasionally many ex-

TABLE 3

RELATIVE FREQUENCIES OF IIA ELEMENTS FROM DIFFERENT POSITIONS IN CALL SERIES, EXPRESSED AS PERCENTAGE OF THE HIGHEST FREQUENCY ELEMENT FROM A GIVEN SERIES

IIA element position	N	$\bar{x}$	±SD	CV
1	78	100	±0.0	—
2	64	92.8	±4.2	4.5
3	45	91.5	±2.9	3.2
4	23	88.2	±3.2	3.6
$A^{A/C}$	71	78.6	±7.4	9.5

changes were made and chorused by many members of the flock. Analysis of the behavioral contexts of call types (Table 4) shows a significantly non-random distribution of these call types among the behavioral contexts ($\chi^2 = 73.2$, df = 12, $P < 0.001$). Further, all call categories (columns) showed non-random distributions in the contextual categories ($P < 0.001$ for each column). In only one contextual category (flock fights) were calls used according to their overall abundance ($\chi^2 = 1.08$, df = 3, $P > 0.5$). Otherwise, a non-random sample of calls occurred in each context ($P < 0.01$ for each row except flock fights).

Category III.—Calls of category III were made up of one to four multi-element phrases (Fig. 2L–N). In a sample of 101 calls, six phrase types were recognized, some of which occurred in several variant forms in the population. These types were separated into two divisions on the basis of acoustic structure (division A, four types; division B, two types). The phrase types of division A (Fig. 5) contained three–five basically arch–shaped elements which varied in the details of shape within a given phrase. The elements also varied in frequency but tended to descend within a given series.

Long series of very high frequency (8.5–9.5 kHz), long duration (150–180 msec) elements were frequently interspersed with calls of category III. Series containing type B_2 phrases invariably contained one of these high frequency elements immediately before and after each B_2 phrase. Phrase type A_3 as well as A_1 were often followed by an element of similar shape but much lower in frequency ($\bar{x} = 2.88$ kHz, SD = ±0.75) and longer duration ($\bar{x} = 33.4$ msec, SD = ±4.3).

Phrase types A_1 and B_1 occurred most frequently in the sample (Fig. 6), and call forms containing either or both of these phrases accounted for 55.4% of the recorded forms. Call forms containing more than one

TABLE 4

BEHAVIORAL CONTEXTS OF CATEGORY II CALLS CONTAINING DIFFERENT COMBINATIONS OF ELEMENT TYPES

Context	A only	A–A/C–C[a]	B only	A–B–C[b]	Total
Leaving forage patch	0	5	8	8	21
Arriving in new forage patch	0	15	0	1	16
Vocal exchange after isolation	0	19	0	1	20
Startled, flying up	11	5	4	0	20
Flock fight	5	10	3	2	20
Total	16	54	15	12	97

[a] Combinations A–A/C, A–A/C–C, and A/C–C.
[b] Combinations A–B and A–B–C.

phrase type nearly always (98%) contained a representative from both major divisions. Two call forms, A_1–B_1–B_1 and A_3, constituted 42% of the forms recorded (Fig. 7A). The relatively small number and the discrete nature of the component phrase types in category III calls afforded a virtually complete sampling (Fig. 7B).

Although many variant forms occurred within each of the A type phrases, their pattern of delivery suggested that these variants were stereotyped and individually specific. This was indicated by the observations that, during flock fights, the same phrase type was exchanged in different variants by different individuals. Sample sizes of these calls were too low for statistical evaluation, but, when tracings of calls were overlaid on calls from the same bird later in the same bout, they showed only slight variation in call structure. One variant of A_1 was recorded in the same locality on four different occasions over a period of 2 months. Different variants of A_1 were recorded at three of the five study sites.

Although the sample sizes for the contextual correlates of III calls are too small for statistical testing, certain patterns of usage are apparent (Table 5). Phrase types A_1 and A_3 unassociated with type B phrases had the most distinctive usages. A_1 appears to be associated with an increasing likelihood of an aggressive encounter, A_3 with close aggressive contact. The other phrase types and phrase combinations were given primarily while the callers were more or less isolated from their flocks or while also giving their whistled song (category IV, below).

Category IV.—Calls of this category (whistled song) consisted of two short elements followed by two longer ones (Fig. 2O). All seven observed bouts of singing consisted of this song type interspersed with calls of category III. Recordings of Mountain Chickadee songs from other regions, obtained from the Library of Natural Sounds (Laboratory of Ornithology,

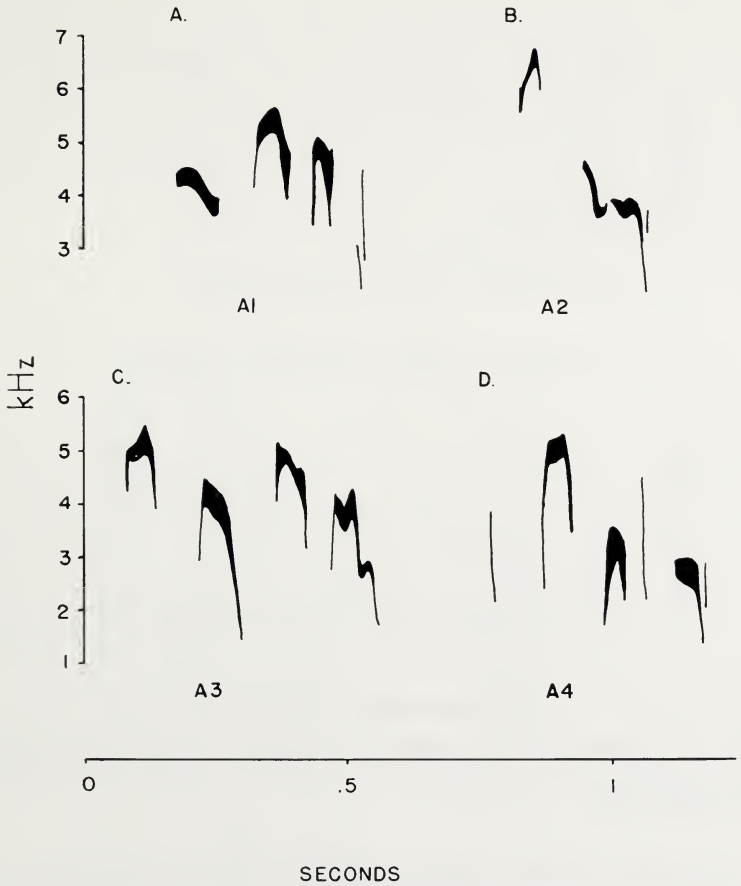

FIG. 5. Representative examples of the four category II division A phrase types.

Cornell University), contained elements at two different frequencies, thus indicating regional dialects.

Courtship, begging, and miscellaneous calls.—The calls given by begging females early in the breeding season and by fledglings during their first few weeks out of the nest contained elements that were structurally similar to those found in the category II calls, but these elements were arranged in reverse order (Fig. 1K).

During two overflights by Cooper's Hawks (*Accipiter cooperii*), chickadees gave very high frequency (9–10 kHz), whistle-like calls. These calls lacked measurable onset or cutoff points, but the duration of single ele-

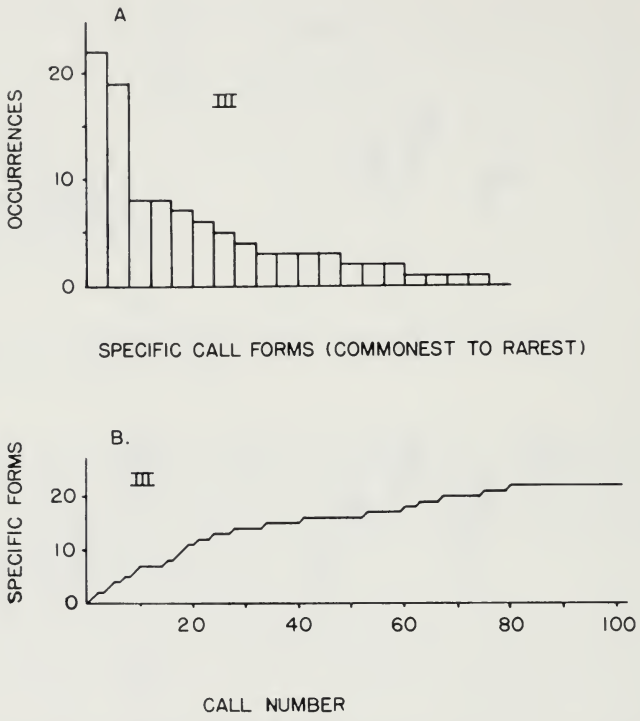

FIG. 6. A, occurrence frequency histogram for specific call forms of category III, arranged in order of abundance in the recorded sample; B, cumulative repertoire size for specific call forms of category III.

ments exceeded 250 msec. Several elements were associated in long series. The Mountain Chickadee is also reported to give a "hissing" call when disturbed in the nest hole (Grinnell et al. 1930).

DISCUSSION

The four major categories of the Mountain Chickadee's vocalizations can be considered to occur in two larger divisions based on patterns of variation. Categories III and IV varied discretely in that they were made up of discrete phrase types (six for category III, one type for category IV), which varied only slightly between occurrences. Intermediates between phrase types did not occur. Categories I and II, however, were made up of element types within which there occurred considerable variation. The various forms in the element types (one type for category I, three types for category II) could be arranged in graded continua. Considerable gradedness occurred within calls of category II as well as between calls of both

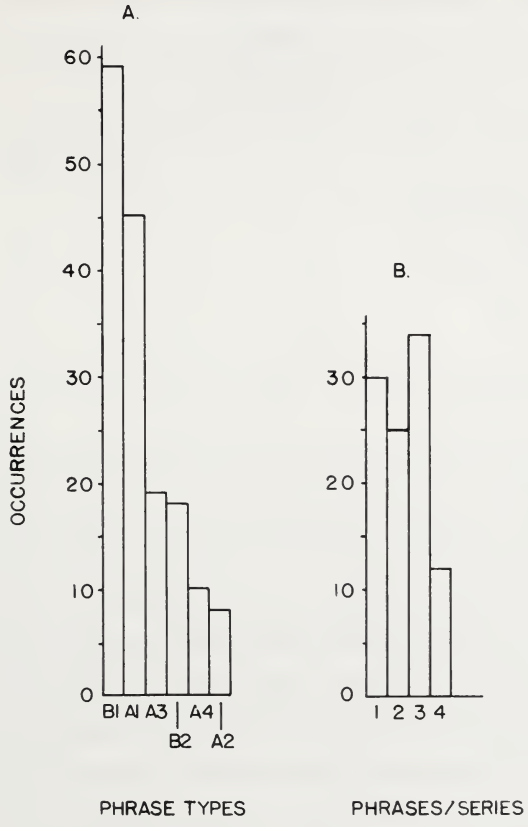

FIG. 7. A, occurrence frequency histogram for specific call forms of category III; B, cumulative repertoire size for specific call forms of category III.

categories I and II. The presence of both continuously and discretely varying categories in the same species' repertoire suggests that the difference is communicatively meaningful. Since distinctive behavioral patterns can be associated with the different vocalization categories, functional correlates of their two patterns of variability may be indicated.

One possible functional correlate of variability patterns could be associated with the greater semantic reliability of discrete signals. The discretely varying calls of categories III and IV were used either for long distance communication, where signal degradation was likely to be a problem, or in aggressive confrontations, where unambiguous signals would be important, either for regulating flock advance or retreat, or for signalling aggressive intentions to opponents. The distances over which the calls of

TABLE 5
BEHAVIORAL CONTEXTS OF CATEGORY III CALLS CONTAINING DIFFERENT PHRASE COMBINATIONS

	A_3	A_1	A_1–B_1–B_1	All other combinations	Total
No apparent provocation, caller isolated	1	2	19	53	75
Approaching flock fight	1	5	0	0	6
Flock fight	14	0	3	0	17
Supplanting attack	3	0	0	0	3
Total	19	7	22	53	101

categories I and II were used, however, were usually not so great that signal degradation was likely to be a problem. Nor were the situations in which the calls were given characterized by an urgent need for a correct response. It thus appears that there is an inverse relationship between the need for reliability and certainty in a signal and its variability; precision of meaning and subtlety of expression are apparently sacrificed to urgency.

The repertoire of the Mountain Chickadee is typical of North American chickadees (Table 6). The vocal repertoires of three species have been described with the aid of the audiospectrograph (Carolina Chickadee [*P. carolinensis*] Smith 1972, Gaddis 1979; Boreal Chickadee [*P. hudsonicus*] McLaren 1976; Black-capped Chickadee [*P. atricapillus*] Ficken et al. 1978). Certain other vocalizations of other chickadee species have also been described (Dixon et al. 1970, Dixon and Martin 1979). With few exceptions, evaluations of quantitative variation are not available, but the comparative material shows that all major call categories except IV, the whistled song, are possessed by the group as a whole. In Mexican (*P. sclateri*), Chestnut-backed (*P. rufescens*), and possibly Boreal chickadees, territorial advertisement is accomplished by vocalizations with the acoustic structure of category III.

Category I calls appear to be most diverse in the Carolina Chickadee. Figures of several variant forms are presented in Smith (1972) and Gaddis (1979). Some of these appear comparable in structure to IIA elements (i.e., high pitched arch), but others appear to be unrelated. For all other species, the category I elements are very similar to the category IIA. The two species with frequency modulated IIA calls, the Mexican and Chestnut-backed chickadees, also have frequency modulated I calls. In all species, these category I calls were used as close-range, contact calls.

In category II, all three element types and fused A/C elements are

TABLE 6
VOCAL REPERTOIRES OF NORTH AMERICAN CHICKADEES

	P. gambeli	*P. carolinensis*	*P. atricapillus*	*P. sclateri*	*P. hudsonicus*	*P. rufescens*
I	+[1]	+[2,3]	+[1,4,7]	+[1]	+[6,7]	+[1,7]
IIA	+[1,7]	+[2,3]	+[1,4,7]	+[1,5]	+[6,7]	+[1,7]
IIB	+[1]	+[2,3]	+[1,7]	+[1]	+[6,7]	+[1,7]
IIC	+[1,7]	+[2,3]	+[1,4,7]	+[1,5]	+[6,7]	+[1,7]
IIA/C	+[1,7]	+[3]	+[7]	+[1]	+[6,7]	+[1,7]
Alarm whistle	+[1]	+[2,3]	+[4]	+[1]	+[6]	+[1]
III	+[1,7]	+[2,3]	+[1,4,7]	+[1,5]	+[6,7]	+[1,7]
IV	+[1,7]	+[2,3]	+[1,4,7]	−[1,5]	−[6]	−[7]
"Hiss"	+[8]	+[8]	+[8]	?	+[6]	+[8]

[1] Pers. obs. and recordings.
[2] Smith 1972.
[3] Gaddis 1979.
[4] Ficken et al. 1978.
[5] Dixon and Martin 1979.
[6] McLaren 1976.
[7] Recordings from Library of Natural Sounds, Laboratory of Ornithology, Cornell University.
[8] Sibley 1955.

present in the repertoires of all six species. In all species, the pattern of element type arrangement is the same, i.e., A before B before C. Furthermore, runs of A elements descend in frequency in all species.

Neither the high whistle alarm calls nor the high pitched elements associated with the category III calls of the Mountain Chickadee appear to fit well into any of the four categories. However, both may be related to IIA calls. Series containing only IIA elements were typically associated with circumstances of at least mild alarm, and here the successive elements occasionally ascended in frequency while also becoming longer in duration. These ascending series did not quite attain the frequencies of alarm calls, but occasionally had frequencies and structures of the elements associated with the category III calls. Carolina Chickadees possess alarm calls, which are very similar to, and probably homologous with those of the Mountain Chickadee. Category IIA calls of Carolina Chickadees, when used in circumstances of comparable apprehensiveness, often contained the full range of graded intermediates between IIA elements and the high whistle alarm calls, thus indicating a relatedness of these alarm calls to category IIA.

Calls with the general acoustic structure of category III occur in the repertoires of all six species. In the Mountain and Mexican chickadees, category III calls appear to be highly stereotyped with individuals possessing repertoires of several forms.

The high frequency elements that are frequently interspersed into bouts of category III calls of the Mountain Chickadee are also given by Carolina, Black-capped, and Mexican chickadees. These high frequency elements are referred to as "Variable See" in the repertoires of the Carolina (Smith 1972) and Black-capped chickadees (Ficken et al. 1978), and appear to be used comparably to those of the Mountain Chickadee.

Dixon et al. (1970) reported that both male and female Mountain Chickadees from northern Utah gave series of high pitched (>8 kHz) elements during precopulatory interactions. The spectrograms of these calls, however, strongly resemble the high frequency elements that were often interspersed in bouts of category III calls in the Flagstaff population. In Dixon et al.'s (1970) account, these elements ended in a category III call. It appears possible that the calls they recorded during courtship and copulation were not restricted to those activities.

In general, the calls of category III are used in aggressive contexts. They are also frequently mixed into bouts of whistled song in those species which have it, and substituted entirely for whistled song in those species which do not.

Six other species occur in the subgenus *Poecile,* but spectrographic analyses of their repertoires have not yet been made. Various vocalizations from their repertoires have, however, been described. Calls with the structure of category II from three of these species, the Sombre Tit (*Parus lugubris*), the Willow Tit (*P. montanus*) and the Marsh Tit (*P. palustris*) are figured in Thielcke (1968) and Latimer (1977). These calls contain elements of types A and C arranged according to the same pattern as in the North American species. The Marsh Tit and the Willow Tit both possess territorial advertisement calls that are very different from those of the North American species. According to Thönen's (1962) verbal transcriptions, the Willow Tit also has calls of categories I; II with element types A, B, and C; a high frequency alarm call; and III. Moreover, except for some territorial advertisement calls, the Willow Tit appears to have a typical chickadee repertoire.

According to the verbal descriptions of the vocalizations of the Marsh Tit (Morley 1953), it appears that this species possesses several other calls besides those shown in Thielcke (1968) and Latimer (1977) that are comparable in structure and usage to the other chickadees. These calls include a single element call used for close-range contact, a high whistle alarm call, a multi-element series that appears comparable to IIA–C, and calls that appear to be comparable to III and used in aggressive situations.

It thus appears that there is a generalized chickadee repertoire, with category II representing a conservative core. Interspecific differences in

this category occur, primarily in element duration, but the same element types are widespread and are arranged according to a common syntax.

SUMMARY

The vocal repertoire of the Mountain Chickadee (*Parus gambeli*) is described with particular emphasis on the quantitative evaluation of variability patterns. The vocalizations were separated into four major categories: single element, close-range, contact calls (category I); multi-element, mid-range, contact calls (category II); threat calls consisting of rearrangeable, stereotyped phrases (category III); and whistled songs (category IV). The arrangement of elements in category II calls was tightly restricted by simple rules, but the number of potentially distinctive call forms was nevertheless large. The threat calls (category III) appeared to consist of a small number of stereotyped phrases, whose arrangement was also restricted by simple rules.

A comparative review of vocal repertoire organization in all North American chickadees, except the Alaskan form of the Siberian Tit (*P. cinctus*), shows that each of the six species possesses categories I, II, and III. Three species lack the whistled song. All three element types of category II are possessed by the six species and are expressed according to a common syntax.

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GEORGE MIKSCH SUTTON AWARD FOR ORNITHOLOGICAL ART

The Wilson Ornithological Society announces the establishment of the George Miksch Sutton Award for Ornithological Art. The Award will be given for art that would be suitable as a color plate in The Wilson Bulletin. The subject matter and medium are at the artist's discretion. Size of the artwork should be no smaller than 9¼ × 14 inches high and no larger than 18⅜ × 27¾. Any artist who has not been represented by a major gallery or who has not been featured in magazines such as Audubon or National Wildlife is eligible to enter. Prior publication of a color plate in a professional journal does not disqualify an artist. In short, the competition is primarily for artists who do not make their living, or a significant portion of it, by painting birds. Artists who question their eligibility should query the Award Committee when requesting entry information. Artwork will be judged by a panel of ornithologists and artists at the June 1985 Wilson Ornithological Society/Cooper Ornithological Society joint annual meeting in Boulder, Colorado. All qualified entries will be on display at the meeting. Artists should insure their entries both to and from the meeting and include a return mailer with postage attached. Matting and/or framing is at the discretion of the artist. The winner of the competition will receive a check for $500, and his/her artwork will appear as a color plate in The Wilson Bulletin. For further information and application form, contact **Phillips B. Street, Chairman, Sutton Award Committee, Lionville Station Road, R. D. 1, Chester Springs, Pa. 19425.**

Wilson Bull., 97(1), 1985, pp. 47–56

VARIATION IN THE SONGS OF FEMALE BLACK-HEADED GROSBEAKS

GARY RITCHISON

The examination and description of variation in the songs of passerines have been the objects of numerous studies in recent years (Thielcke 1969, Nottebohm 1975, Krebs and Kroodsma 1980). These studies have dealt almost entirely with variation in the songs of males, which is understandable since singing by females is not as widespread. There are a few species, however, in which females do sing on a regular basis. For example, singing by females has been reported in the Northern Cardinal (*Cardinalis cardinalis*) (Laskey 1944, Lemon 1965), Rose-breasted Grosbeak (*Pheucticus ludovicianus*) (Ivor 1944, Dunham 1964), Northern Oriole (*Icterus galbula*) (Beletsky 1982), Red-winged Blackbird (*Agelaius phoeniceus*) (Beletsky 1983), and several other species (Armstrong 1963, Van Tyne and Berger 1976). Despite these reports of singing by female songbirds, there have been few, if any, studies that have provided a detailed examination of female song in a species. In the present study I examined intra- and interindividual variation in the songs of a population of female Black-headed Grosbeaks (*Pheucticus melanocephalus*).

STUDY AREA AND METHODS

I recorded female Black-headed Grosbeaks at Malibu-Guinavah Forest Camp (Cache National Forest), 10 km east of Logan, Cache Co., Utah. Individual females were captured in mist nets and provided with a unique color band combination to aid in individual recognition.

Songs were recorded during the breeding seasons of 1977 and 1978 using a Nagra IIIB tape recorder with an Altec 633A microphone mounted on a 62-cm parabolic reflector. Sonagrams of the songs were produced using a Kay Elemetrics 6061B Sona-Graph with the wide-band filter setting. These sonagrams were then examined to determine several quantitative parameters of individual songs, i.e., syllables per song, syllables/kind (the number of syllables in a song divided by the number of kinds of syllables in that song), and duration. I also determined the number of syllable types present in each female's repertoire and the patterns of similarity in the songs of females within the population. I define syllable as either a continuous tracing on the sonagram or a grouping of such tracings that always occurred together. Classifying syllables was difficult at times because of the variation in their form in successive songs. Fig. 1 illustrates the variation in two syllables used by one female grosbeak.

Recordings were made of the songs of 12 females. However, when the total number of syllables was graphed cumulatively against the total number of songs sampled, the curves were asymptotic for only five birds. Thus, only these five birds were used when determining the average syllable repertoire.

It was possible to compare the syllables of any female according to their similarity with

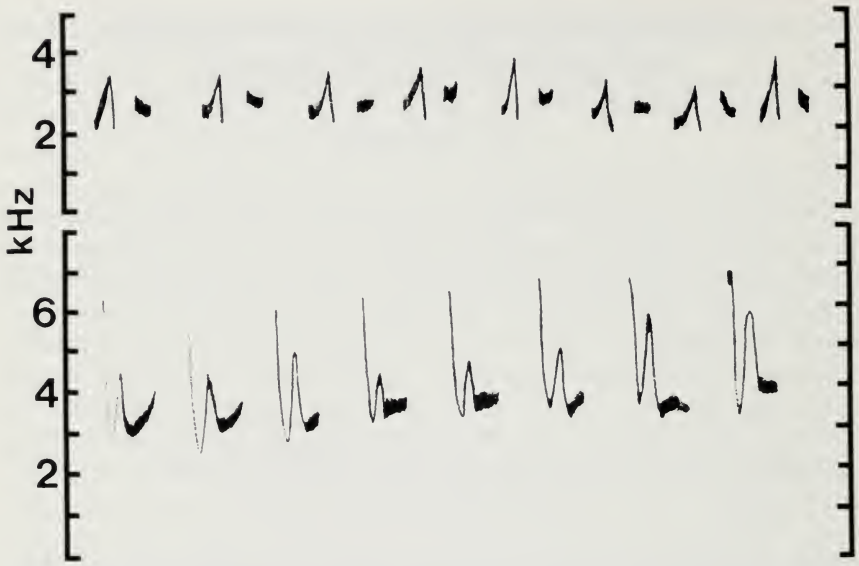

FIG. 1. Variation in the form of two syllables in the songs of a female Black-headed Grosbeak.

those of other females or males, thereby obtaining an indication of the overlap of syllable repertoires. The amount of syllable sharing between two grosbeaks was assessed by a formula derived by Harris and Lemon (1972):

$$\frac{2 \times \text{no. of syllables common to both repertoires} \times 100}{\text{Total syllables of bird 1 + total of bird 2}}$$

RESULTS

The songs of female Black-headed Grosbeaks consisted of syllables of varied frequency lying between 1.5 and 5.0 kHz (Fig. 2). The mean number of syllables per song was 4.5 ± 1.8 and the mean song duration was 1.47 ± 0.41 sec (Table 1). An analysis of the songs of 24 male grosbeaks (N = 545) revealed an average of 10.3 ± 3.5 syllables per song while the mean song duration was 3.5 ± 1.3 sec. These differences between the songs of males and females were found to be significant ($P < 0.01$, *t*-test). Individual syllables utilized by females had a mean duration of 0.15 ± 0.03 sec (N = 126) while the mean intersyllable interval was 0.12 ± 0.02 sec (N = 200). A catalog of tracings from 264 audiospectrograms was used to distinguish a total of 126 different syllables (Figs. 3 and 4). The number of different syllables in the repertoires of the females studied ranged from 5 to 28 (Table 1).

Female grosbeaks showed a pronounced tendency to use a few of the

TABLE 1

SYLLABLE AND DURATION CHARACTERISTICS OF SONGS OF FEMALE GROSBEAKS

	No. of songs analyzed	No. of syll.[b] in repertoire	No. syll./song ($\bar{x}$ ± SD)	Song duration in sec ($\bar{x}$ ± SD)
1977				
Red I[a]	28	(14)	7.5 ± 2.6	2.26 ± 0.77
Bridge	26	(15)	5.5 ± 1.2	1.21 ± 0.28
Island	11	14	4.5 ± 2.4	1.13 ± 0.52
UB	47	(28)	5.7 ± 1.3	1.60 ± 0.22
Riverside	42	(5)	4.0 ± 1.3	1.32 ± 0.36
Guinavah	15	11	5.3 ± 1.7	1.29 ± 0.35
Ballfield	8	14	4.1 ± 1.1	1.34 ± 0.35
Black	3	7	3.3	0.85
1978				
cs 28	39	(26)	5.2 ± 1.6	1.21 ± 0.39
LM	11	15	5.4 ± 1.8	1.14 ± 0.38
Red I[a]	25	(12)	6.5 ± 1.5	1.90 ± 0.48
East Ballfield	7	4	6.1 ± 1.1	1.32 ± 0.27
AL	2	4	4.0	0.92
	264	$\bar{x}$ = 16.7	4.5 ± 1.8	1.47 ± 0.41

[a] Same female recorded in different years.
[b] Only those numbers in parentheses were used to determine average.

syllables from their total repertoires much more than other syllables. For example, one female uttered a total of 211 syllables in 28 songs. Although this female had a repertoire of 14 syllables, three syllables made up 82.0% of the total. Another female uttered 196 syllables in 38 songs and two syllables (out of a total syllable repertoire of 26) made up 56.6% of this total. Four syllables made up 73% of the total. This tendency to repeat syllables was also apparent when songs were analyzed in terms of syllables/kind. Analysis of the songs of eight females (10 songs/female) revealed a mean value of 1.41 ± 0.22. Similar analysis of the songs of their mates gave a mean value of 1.02 ± 0.02, a significantly lower value ($P < 0.001$, t-test).

Sharing of syllables among females was uncommon. Ninety-nine of the 126 syllables (78.6%) were limited to one female's repertoire. Furthermore, 21 syllables (16.7%) were found in the repertoires of just two females, and five syllables (4.0%) were noted in the repertoires of three females. The remaining syllable was found in the repertoires of seven females. In contrast, syllable sharing among males appeared to be more common. For example, the songs of six of seven males present in the

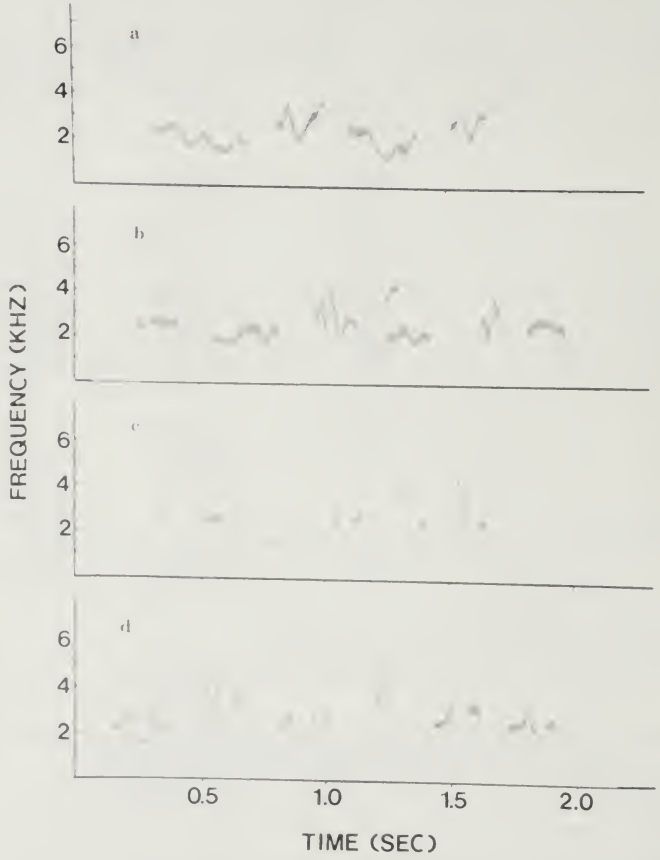

FIG. 2. Representative songs of four female Black-headed Grosbeaks.

Malibu-Guinavah study area in 1978 typically began with the same four syllables. Furthermore, the songs of five of these males typically began with the same six syllables (Ritchison 1980).

A catalog of the syllables in the repertoires of 22 male Black-headed Grosbeaks was also prepared (Ritchison 1980) and a comparison of the 156 syllables used by males with those used by females revealed that there was some sharing of syllables between the sexes. Approximately one-fourth of the syllables used by females resembled those found in the repertoires of the males. Much of this sharing between the sexes (60.5%) was the result of females using syllables similar to those of their mates.

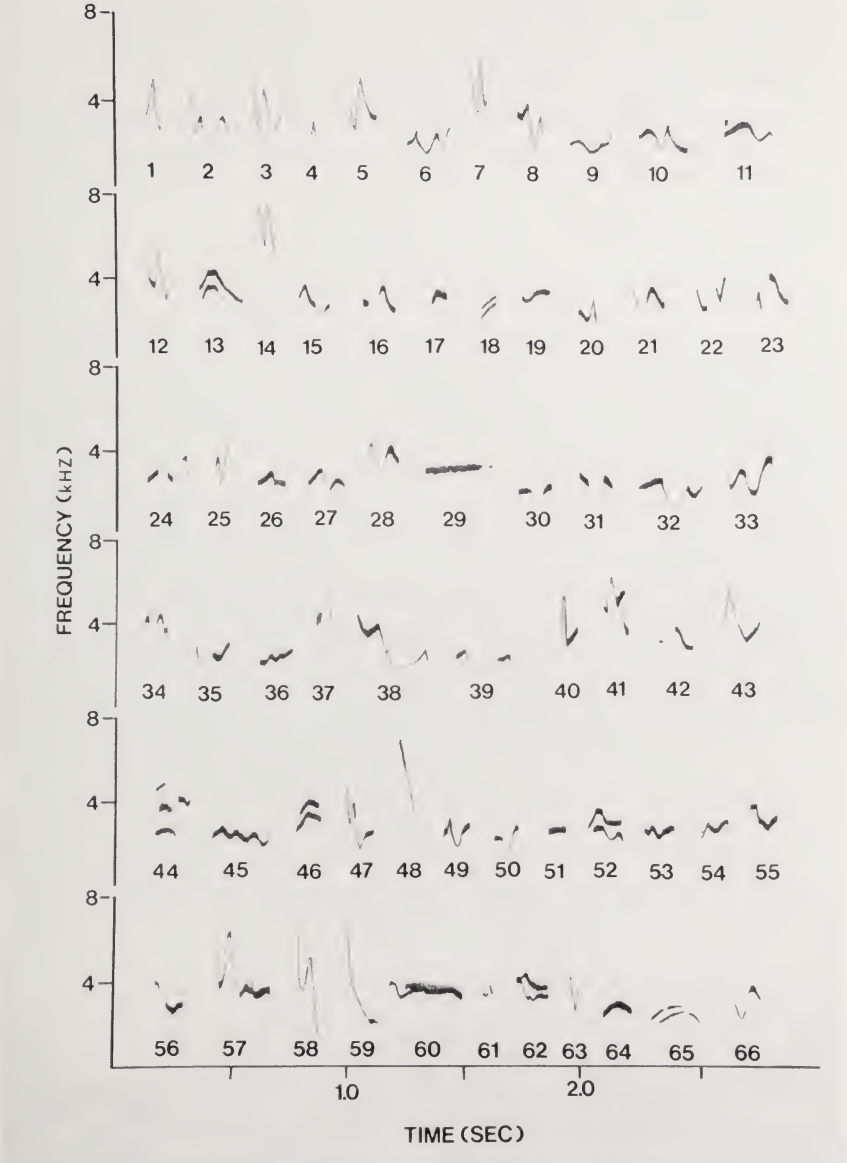

FIG. 3. Catalog of syllable types of female Black-headed Grosbeaks (Syllables 1–66).

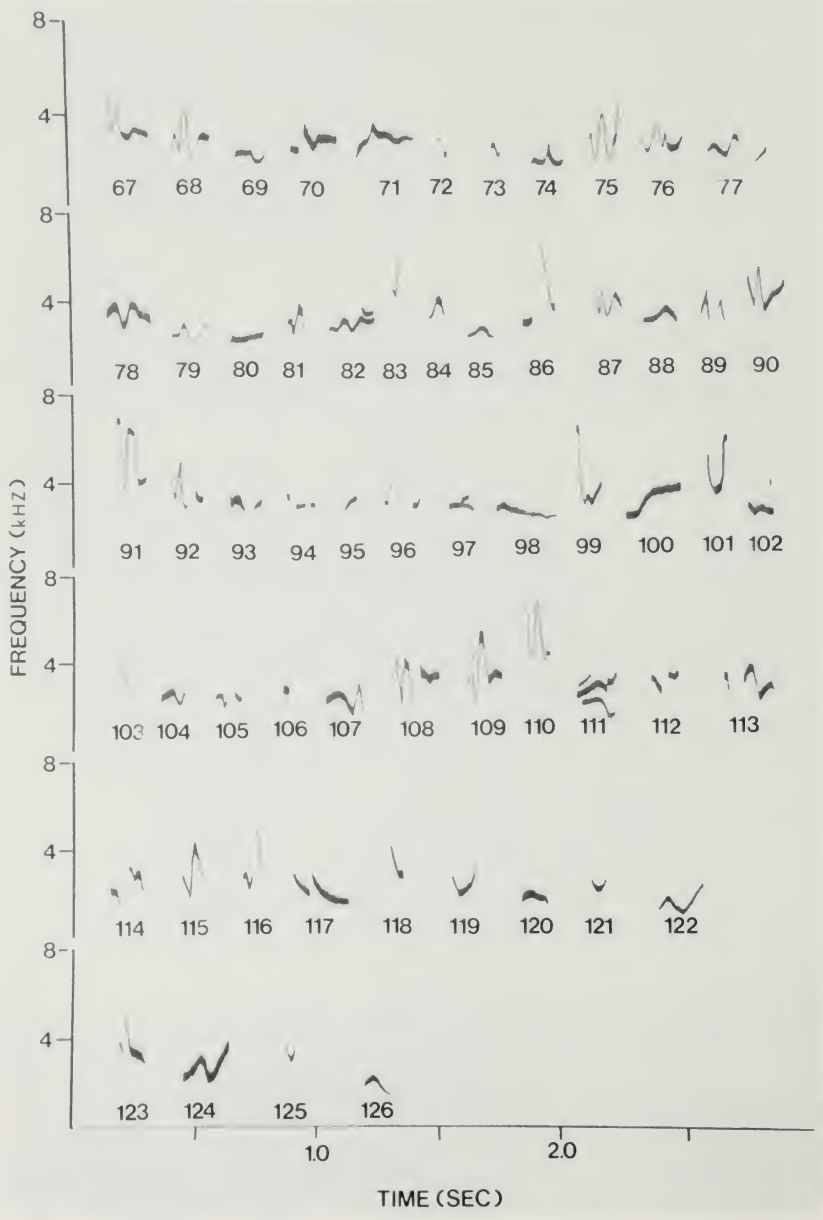

FIG. 4. Catalog of syllable types of female Black-headed Grosbeaks (Syllables 67–126).

DISCUSSION

The songs of female Black-headed Grosbeaks appear to differ in certain respects from the songs of many male songbirds. One such difference is that females do not accurately reproduce specific syllable types in successive songs. Several studies have illustrated the consistency with which many male songbirds reproduce specific syllable types (Kroodsma 1975, Lein 1978, Martindale 1980, Chew 1981). However, highly variable syllable types or song types have been reported in male songbirds during song development (i.e., plastic song) and in canaries (*Serinus canarius*) when males begin to sing again after a period of several months when they sing very little or not at all. Nottebohm (1981:1368) noted that at the end of this period the "male canaries start to sing once more . . . in the tentative, highly variable manner typical of early plastic song." Nottebohm (1981) suggested that such variability may be related to low levels of testosterone in the blood and the effect of these low levels on the areas of the brain that control singing behavior. The variable nature of the syllables produced by female Black-headed Grosbeaks could similarly be due to low testosterone levels. Previous investigators have suggested that hormone levels may influence the singing behavior of females in other species. Falls (1969:210) noted differences in the songs of male and female White-throated Sparrows (*Zonotrichia albicollis*) and indicated that the songs of females are often "short, quavering and variable in speed . . . [and] lack the precise control of pitch and timing characteristic of males." He further suggested that these qualities in the songs of females may be a function of the low levels of testosterone in females.

Recent evidence indicates that differences in the central nervous systems of males and females may contribute to differences in behavior. For example, Nottebohm and Arnold (1976) noted sexual dimorphism in the song control areas of the brain of canaries which appears to be related to differences in the singing behavior of males and females. Adult male canaries have a complex song repertoire while females normally do not sing. Even when testosterone is administered, females sing a less complex song than do males. Such dimorphism may contribute to some of the differences in the songs of male and female Black-headed Grosbeaks. That is, the songs of males were more "complex" in terms of the number of syllables per song, kinds of syllables per song, and duration.

The results of the present study indicate that individual female Black-headed Grosbeaks possess syllable repertoires that are largely unique. Furthermore, female grosbeaks apparently possess rather limited "functional" repertoires, with only a limited number of syllables out of the total repertoire normally being used. Such small and largely unique rep-

ertoires suggest that individual recognition may be of importance to female grosbeaks (Harris and Lemon 1972, Falls 1982). This appears to be the case since the songs of females apparently are important in family-group maintenance (Ritchison 1980, 1983a).

As noted above, analysis revealed several differences between the songs of male and female Black-headed Grosbeaks. Furthermore, playback experiments have shown that both sexes apparently use such differences to differentiate between the songs of males and females (Ritchison 1983b). The possible significance of such differentiation has been discussed by various authors. For example, singing by female White-crowned Sparrows (*Z. leucophrys*) reportedly is confined to the early part of the breeding season (Blanchard 1941, Kern and King 1972, Baptista 1975). Baptista (1975) suggested that such singing behavior is probably adaptive because the songs of these females are similar to those of males and such songs evoke aggressive behavior from territory-holding males. Early in the breeding season white-crown males are less aggressive and respond weakly, if at all, to playback of recorded songs. The lack of response by territorial males to the songs of female grosbeaks appears to be equally adaptive. That is, after the young fledge, family groups begin to wander and female grosbeaks use their songs to maintain contact. If the songs of females were similar to those of males and evoked aggressive behavior from territorial males, then females would risk being chased or attacked each time they sang. Under such conditions, maintaining contact with young grosbeaks would be difficult or impossible.

SUMMARY

Although numerous investigators have examined variation in the songs of male passerines, there are few descriptions of such variation in the songs of females. In the present study I examined intra- and interindividual variation in the songs of female Black-headed Grosbeaks (*Pheucticus melanocephalus*). The songs of individual females consisted of a series of syllables of varied frequency lying between 1.5 and 5.0 kHz. The mean number of syllables per song was 4.5 and the mean song duration was 1.47 sec. The number of syllables in the repertoires of female grosbeaks ranged from 5–28.

The songs of female grosbeaks differed from the songs of males in that females appeared unable to reproduce consistently specific syllable types as accurately as males and the songs of females were less complex than the songs of males. Such differences may be due to differences in the levels of testosterone found in males and females. Previous investigation suggests that this hormone affects the development and maintenance of areas in the brain that control singing behavior.

Sharing of syllables among females was uncommon with 78.6% of all syllables limited to the repertoire of one female. Such distinctiveness generally indicates that individual recognition may be important. Young grosbeaks appear to recognize parental songs and use this ability to maintain contact with their parents after fledging.

ACKNOWLEDGMENTS

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DEPT. BIOL., UMC 53, UTAH STATE UNIV., LOGAN, UTAH 84322. (PRESENT ADDRESS: DEPT. BIOL. SCI., EASTERN KENTUCKY UNIV., RICHMOND, KENTUCKY 40475.) ACCEPTED 16 OCT. 1984.

JOINT MEETING OF THE WILSON AND COOPER ORNITHOLOGICAL SOCIETIES

The Fourth Joint Meeting of the Cooper and Wilson Ornithological Societies will be held 5–9 June 1985 at the University of Colorado, Boulder. A 3-day scientific program is scheduled with contributed papers and several half-day mini-symposia. Morning field trips are planned to ponderosa pine stands in the foothills, water bird habitats and heronries on the prairie, and open meadows, coniferous and aspen forests in the mountains. All day trips on 9 June will tour Rocky Mountain National Park or Pawnee National Grassland. Tours of interest are scheduled for non-ornithological spouses/guests. The banquet will be at the Denver Museum of Natural History. The meeting announcement will be mailed in January; abstracts are due by 6 March. Questions can be directed to CYNTHIA CAREY (Local Committee on Arrangements) or CARL BOCK (Scientific Program) at Department of EPO Biology, Univ. of Colorado, Boulder, Colorado 80309.

Wilson Bull., 97(1), 1985, pp. 57–70

EVENING ROOSTS OF THE SNAIL KITE IN FLORIDA

PAUL W. SYKES, JR.

The wide-ranging Snail Kite (*Rostrhamus sociabilis*) of the New World uses communal night roosts, often in close association with herons and other colonial waterbirds (Bent and Job 1904, Howell 1932, Haverschmidt 1954, Brown and Amadon 1968). Little information has been published on kite roosting sites and roosting habits. In this paper I report on kite roost locations, size, frequency and range of use, time of arrivals and departures, types of habitats, and species associates at roosts in peninsular Florida.

METHODS

I observed evening roosts of the Snail Kite from 1968 through 1980, with the majority of the data collected between 1974 and 1980, primarily during annual Snail Kite censuses in November and December (Sykes 1979, 1982, 1983a). I initially located roost sites by following kites in late afternoon. Observations were generally made between 16:00 and 18:00, after which it was too dark to see the birds without artificial light. For each individual I recorded arrival time to the nearest minute, its plumage type (gray—adult and subadult males, brown—all females and immature males, and unknown—light conditions or distance prevented identification to plumage type; see Sykes [1979]), direction of arrival or departure, and whether or not it had a snail in its bill or had recently eaten as indicated by a distended crop.

Arrival times were standardized to minutes before and after sunset for Miami (U.S. Naval Observatory Nautical Almanac Office 1977) and grouped by plumage type and 5-min intervals before and after sunset. A few morning departure times were recorded. Sky conditions were recorded as either clear (less than 25% cloud cover) or cloudy (26–100% cloud cover).

The study areas are shown in Fig. 1 and roost sites in Figs. 2 and 3. Roosts at each locality were numbered separately, generally from north to south.

RESULTS AND DISCUSSION

Fifty-three percent of the 36 roosts (Figs. 2 and 3, Table 1) studied were in Conservation Area 3A (CA3A) where the major portion of the kite population has occurred during the last 10 years of the study (Sykes 1979, 1983a, b, 1984). Four (11%) of the roosts were occupied for 6 years or more, of which 20 (56%) also were used as nesting sites (Table 1). Most of the larger roosts were occasionally used during the day as loafing sites and feeding perches. The tendency of the species to move in response to changing habitat conditions (Sykes 1979, 1983a, b) perhaps explains why

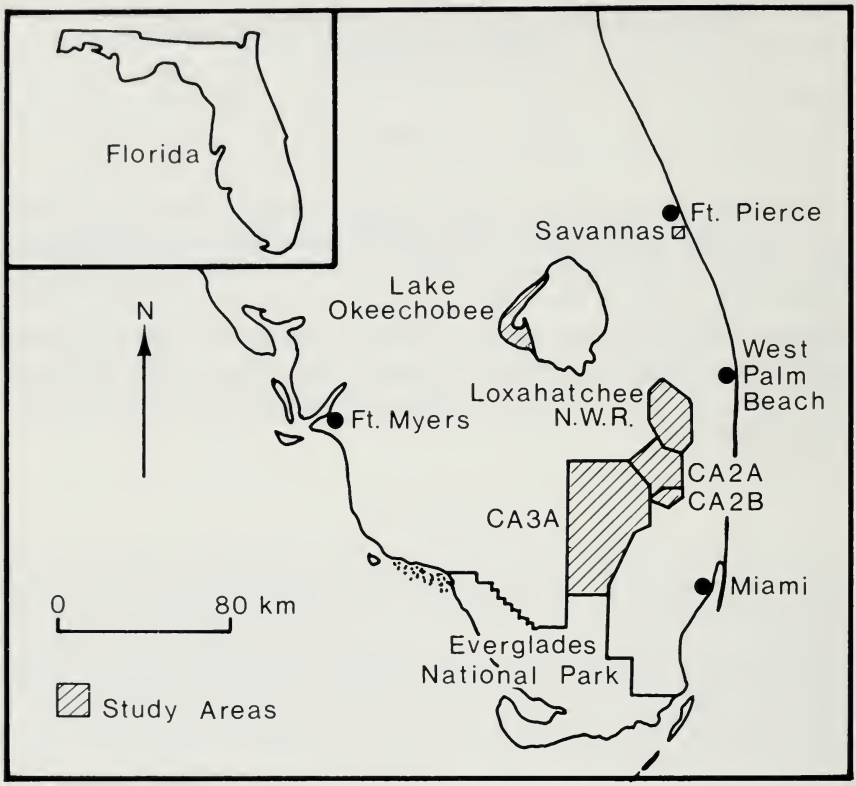

FIG. 1. Study areas in Southern Florida: the Savannas at Ft. Pierce (St. Lucie County); marshes on the west side of Lake Okeechobee (Glades County); and the Everglades (Loxahatchee National Wildlife Refuge [N.W.R.] [Palm Beach County]; Conservation Area 2A [CA2A] [Broward and Palm Beach counties]; Conservation Area 2B [CA2B] [Broward County]; and Conservation Area 3A [CA3A] [Broward and Dade counties]).

89% of the roosts were used for only 3 years or less. The number of kites using a roost varied from 2–85% year to year and ranged from 1 to 113 individuals (Table 1).

All roosts were located in flooded freshwater marshes. Thirty-three (91.6%) of the roosts were in stands of coastal-plain willow (*Salix caroliniana*), two (5.6%) were in stands of the introduced punk-tree (*Melaleuca quinquenervia*) (roost No. 6 in Conservation Area 2A [CA2A] and No. 2 in Conservation Area 2B [CA2B]), and one (2.8%) was in a stand of pond cypress (*Taxodium ascendens*) (roost No. 19 in CA3A). Roost sites were in trees or tall shrubs that formed taller distinctive vegetation units surrounded by low profile sedge-rush marshes of sawgrass (*Cladium jamai-*

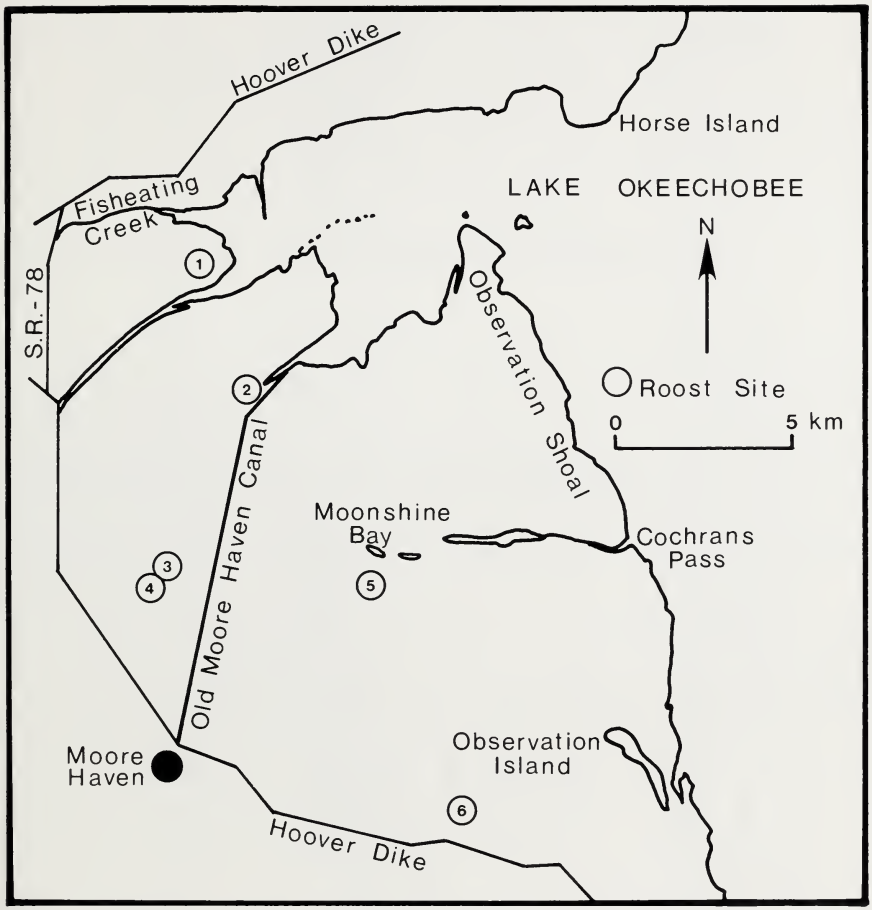

FIG. 2. Roost sites of the Snail Kite in the marshes on the west side of Lake Okeechobee.

censis), wet prairies, or aquatic white water-lily (*Nymphaea odorata*) slough communities.

Willow stands, which grow in thickets, clumps (Fig. 4), or elongated strands, were generally located on the berms around old alligator holes, burned-out peat pockets, former tree island sites, borders of tree islands, or disturbed areas along dikes. Loveless (1959) explains the terms and describes the plant communities. The heights of willows (N = 29) that kites used for roosting ranged from 1.8–6.1 m ($\bar{x}$ = 3.9, SD = 1.1), and the area of the stands ranged from 0.02–5 ha ($\bar{x}$ = 1.7, SD = 1.8). The interior of some willow stands had small openings (Fig. 5), while others were tangles of crooked leaning tree trunks and branches. Kites tended

TABLE 1

SNAIL KITE USE OF EVENING ROOSTS IN FLORIDA, 1968–1980

Roost locality	Roost no.	No. years roost checked	No. years used by kites	Number of individuals using each roost by plumage type												Also used for nesting
				Gray			Brown			Unknown			Total			
				Max.	Min.	$\bar{x} \pm SD$	Max.	Min.	$\bar{x} \pm SD$	Max.	Min.	$\bar{x} \pm SD$	Max.	Min.	$\bar{x} \pm SD$	
Savannas	1	6	3	1			2	1	1.5 ± 0.70	0			3	1	2.0 ± 1.40	X
Lake	1	2	1	3			12			25			40			
Okeechobee	2	1	1	4			15			6			25			
	3 & 4	2	2	10	2	6 ± 5.66	36	12	24 ± 16.97	4			46	20	33 ± 18.38	
	5	1	6+	2			5			58			65			X
	6	2	3	21	6	13.5 ± 10.58	25	13	19 ± 8.48	69			88	46	67 ± 29.70	X
Everglades																
Loxahatchee	1	7	2	14	1	8 ± 4.98	7	2	4.3 ± 2.57	2			23	3	8.7 ± 6.87	X
N.W.R.	2	3	1	4			2			6			12			X
CA2A	1	1	1	5			8			0			13			X
	2	3	2	4	3	3.5 ± 0.71	6			0			10	9	9.5 ± 0.71	X
	3	3	2	10	8	9 ± 1.41	26	20	23 ± 4.24	0			34	30	32 ± 2.83	X
	4	3	2	8	4	6 ± 2.83	17	12	14.5 ± 3.46	0			25	16	20.5 ± 6.32	X
	5	3	1	5			15			0			20			X
	6	3	1	3			6			0			9			
CA2B	1	1	1	2			47			0			49			
	2	3	2	10	3	6.5 ± 4.90	49	34	41.5 ± 10.50	6			65	38	51.5 ± 19.08	
CA3A	1	3	1	3			3			0			6			X
	2	2	1	2			60			0			62			
	3	2	2	6			25	20	22.5 ± 3.46	0			31	20	25.5 ± 7.75	
	4	1	1	5			14			0			19			X
	5	1	1	0			1			0			1			
	6	1	1	4			9			0			13			X

TABLE 1
CONTINUED

Roost locality	Roost no.	No. years roost checked	No. years used by kites	Number of individuals using each roost by plumage type												Also used for nesting
				Gray			Brown			Unknown			Total			
				Max.	Min.	$\bar{x} \pm SD$	Max.	Min.	$\bar{x} \pm SD$	Max.	Min.	$\bar{x} \pm SD$	Max.	Min.	$\bar{x} \pm SD$	
	7	6	6	12	6	7.8 ± 2.24	47	5	16.3 ± 15.64	7	1	4 ± 2.45	59	13	26.8 ± 17.04	X
	8	6	1	8			7			0			15			
	9	1	1	0			4			0			4			
	10	1	1	0			3			0			3			
	11	1	1	0			13			0			13			X
	12	1	1	0			0			4			4			
	13	1	1	0			1			0			1			
	14	2	1	4			3			3			10			X
	15	1	1	2			6			0			8			X
	16	1	1	1			1			1						
	17	6	6+	29	11	18.7 ± 7.22	78	5	27.7 ± 26.56	17	1	5.8 ± 6.18	113	17	52.2 ± 33.94	X
	18	7	6	16	2	10.2 ± 5.57	73	7	30.3 ± 27.42	8	1	2.5 ± 2.79	91	15	43 ± 30.07	X
	19	2	2	2			16	6	11 ± 7.07	0			16	8	12 ± 5.66	X

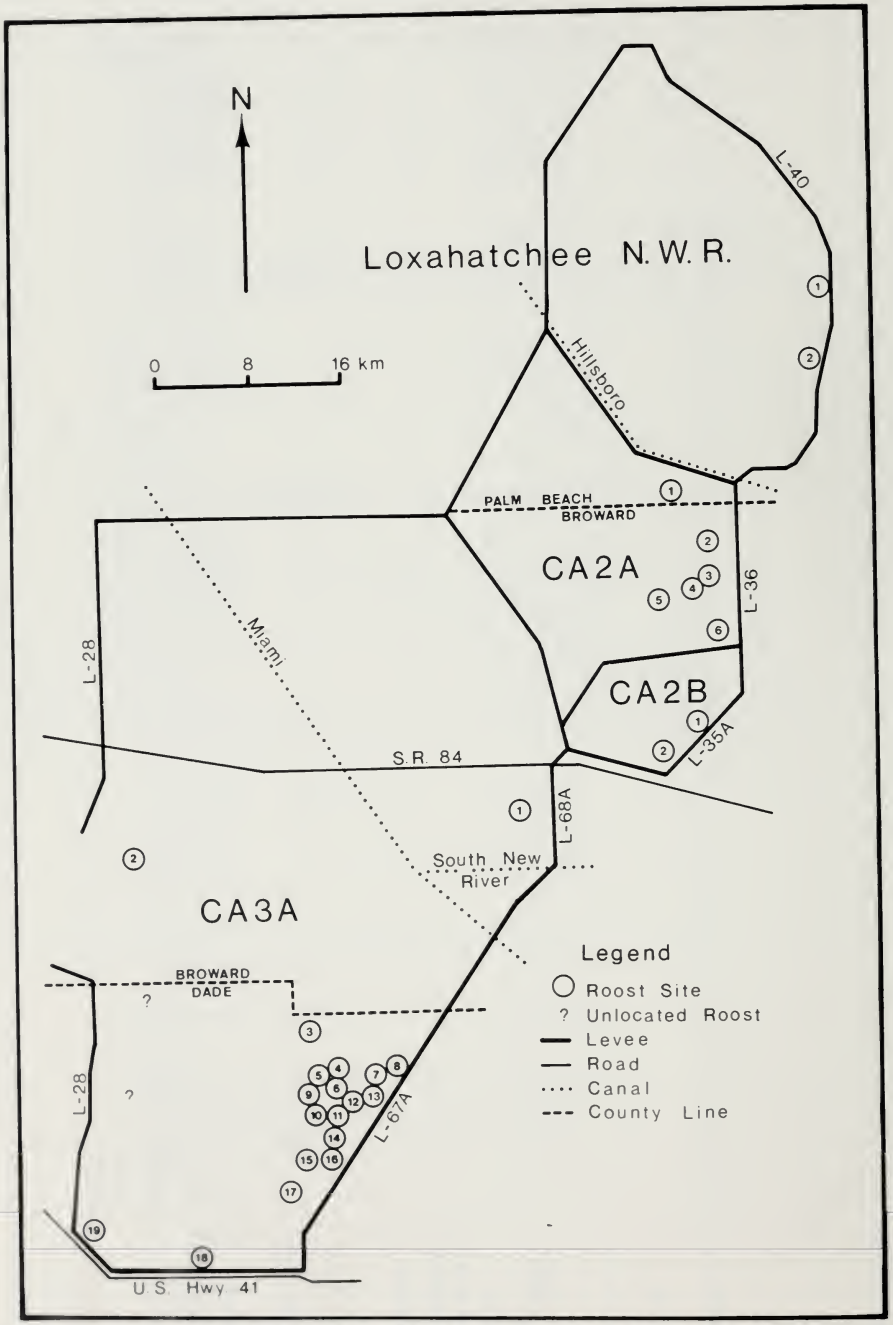

FIG. 3. Roost sites of the Snail Kite in the Everglades.

FIG. 4. Snail Kite roost No. 17 in southeastern CA3A in a large stand of coastal-plain willow. Dense sawgrass is in the foreground. Twelve Anhingas and 41 kites are in flight over the roost and 2 kites are perched to the right of center at the skyline.

to roost around the small openings if present in the stands. In larger stands roosting kites occupied a small area (roughly <10% of the stand). At the punk-tree and pond cypress roost sites the stands were no larger than 0.02 ha with tree heights that ranged from 4–12 m (N = 8, $\bar{x}$ = 8.9, SD = 3.8) and 4.8–8 m (N = 10, $\bar{x}$ = 6.3, SD = 1), respectively. The cypress roost was surrounded by taller trees and was the most "enclosed" of all the sites studied.

While most kites actively hunted immediately before going to roost, some went to the roost site and later departed to forage before returning for the night. This behavior was particularly associated with kites that had arrived at the roost early. In this study, 2–26% of the birds (N = 13 days of observations of 450 individuals, $\bar{x}$ = 0.09, SD = 0.08) arriving at roosts carried snails in their bills, a behavior pattern also reported for Snail Kites in South America (Haverschmidt 1954). Whole snails were usually brought to the roost, but on occasion they had been extracted from the shells. Gray birds brought food to roosts 14% of the time (N = 22) and brown birds 3% (N = 8); however, brown kites arrived with distended crops 46% of the time (N = 135), indicating they had recently fed.

FIG. 5. Inside view of Snail Kite roost No. 17 showing a small opening around an old alligator hole. The photograph was taken in mid-December when coastal-plain willows have dropped their leaves for a 2–3 week period. Ten kites are seen perched during the day.

The estimated heights at which kites flew to roosts ranged from 1.2–91 m (N = 217, $\bar{x}$ = 13.4, SD = 13.4). On calm days or days with relatively light winds 70% of the birds flew to roost at heights of 4.6–30 m (N = 147, $\bar{x}$ = 18, SD = 14). On windy days (winds >16 km/h) birds flying into the wind to the roost generally flew at 1.2–4.5 m (N = 70, $\bar{x}$ = 3.4, SD = 0.8). This difference in the heights at which the kites flew on calm vs windy weather was highly significant (t = 12.6, $P < 0.001$).

Birds arriving at roosts came from all compass directions, but at some sites they appeared to follow specific corridors that tended to follow white water-lily aquatic slough systems.

Kites flew to roost singularly or in loose groups of two to four individuals. Upon arrival at the roost a bird usually would circle before alighting on a tree-top perch, exposed lower branch, or stub. At the roost individuals changed perches, called, sat quietly, preened, or scratched.

In the few cases (N = 9) where I could distinguish the sex and age of arriving birds by eye color, adult females tended to be dominant over both adult males and immatures and often would supplant them from their perches. Adult males would supplant other males and immatures. Individuals usually remained in the upper level of the roost for 10–30

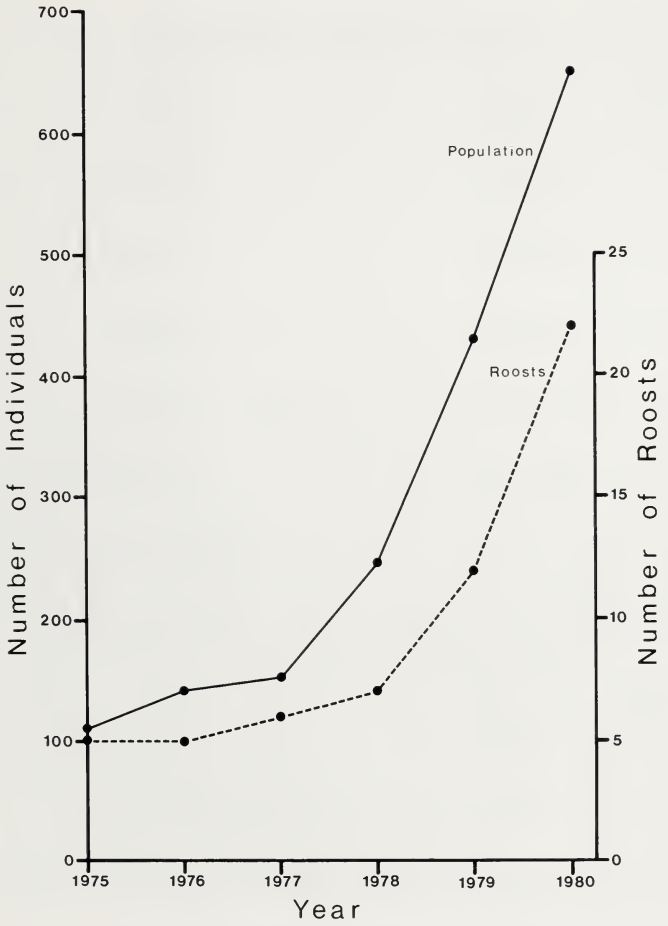

FIG. 6. Relationship of the number of roosts to the Snail Kite population increase, 1975–1980.

min before slowly moving to perches in the middle portion of the vegetation for the night and by darkness all birds had settled into this stratum. In the process of moving to the more sheltered part of the roost, the birds formed tighter groupings. The estimated spacing between roosting birds ranged from 0.3–6.5 m (N = 106, $\bar{x}$ = 0.8, SD = 0.8).

A strong correlation (r = 0.977, P = 0.002) exists between the increase in the kite population and number of roost sites during the 1975–1980 period (Fig. 6). As bird numbers increased during these years of higher water levels (Sykes 1983a), kites began to occupy more of their available

TABLE 2

SPECIES ASSOCIATES AT SNAIL KITE EVENING ROOSTS IN FLORIDA[a]

		% of visits on which species present[b]														
Locality	Roost number	Anhinga (*Anhinga anhinga*)	Great Egret (*Casmerodius albus*)	Snowy Egret (*Egretta thula*)	Little Blue Heron (*E. caerulea*)	Tricolored Heron (*E. tricolor*)	Cattle Egret (*Bubulcus ibis*)	Green-backed Heron (*Butorides striatus*)	Black-crowned Night-Heron (*Nycticorax nycticorax*)	Yellow-crowned Night-Heron (*N. violaceus*)	White Ibis (*Eudocimus albus*)	Glossy Ibis (*Plegadis falcinellus*)	Wood Stork (*Mycteria americana*)	Black Vulture (*Coragyps atratus*)	Turkey Vulture (*Cathartes aura*)	Total species
Savannas	1	X	50		33	33		66								5
Lake	1	X	X		X	X	50	50								6
Okeechobee	2	X			X	X	X	X								5
	3	X	X	X	X	X	X	X	X							8
	4	X	X	X	X	X	X	X	X							8
	5	X	X		X	X		X	X		X					7
	6	X	X	X	X	X	X	X	X		50					9
Loxahatchee	1		71	X	X	X	X		50		50	50				8
N.W.R.	2	X	X		X	66		66	X							6
CA2A	1		X		X	X	X	X								5
	2	X			33	33		33								4
	3	X	X	33	X	66		X	X							7
	4	X			66	66		33	33							5
	5	X	66	33	X	33		33	X							7
	6	X			66	33	33	33	X	X						7
CA2B	1	X		X	X	X	X	X								6
	2	X			33									X	X	4
CA3A	1	X	X	X	X	X		33	X							7
	2		X					33								2
	3	X														1

TABLE 2
CONTINUED[a]

Locality	Roost number	% of visits on which species present[b]															Total species
		Anhinga (*Anhinga anhinga*)	Great Egret (*Casmerodius albus*)	Snowy Egret (*Egretta thula*)	Little Blue Heron (*E. caerulea*)	Tricolored Heron (*E. tricolor*)	Cattle Egret (*Bubulcus ibis*)	Green-backed Heron (*Butorides striatus*)	Black-crowned Night-Heron (*Nycticorax nycticorax*)	Yellow-crowned Night-Heron (*N. violaceus*)	White Ibis (*Eudocimus albus*)	Glossy Ibis (*Plegadis falcinellus*)	Wood Stork (*Mycteria americana*)	Black Vulture (*Coragyps atratus*)	Turkey Vulture (*Cathartes aura*)	
	4	X	X		X	X											4
	5	X			X			33									3
	6	X	X		X	X											4
	7	X	X	83	X	X		X	X								7
	8	X			X	X											3
	9	X															1
	10																0
	11	X						50									2
	12	X															1
	13																0
	14	X															1
	15	X						X									2
	16																0
	17	X	X		X	X		66									5
	18	X	X	86	X	X		X	X		X						8
	19	X	X	X	X	X		50	50		X		X				9
% roosts	—	83	53	31	72	67	25	67	36	3	14	3	3	3	3	—	

[a] Not included: King Rail (*Rallus elegans*), Sora (*Prozana carolina*), Purple Gallinule (*Porphyrula martinica*), Common Moorhen (*Gallinula chloropus*), Limpkin (*Aramus guarauna*), and passerines as they were too inconspicuous to be recorded consistently while counting kites.
[b] X = 100%.

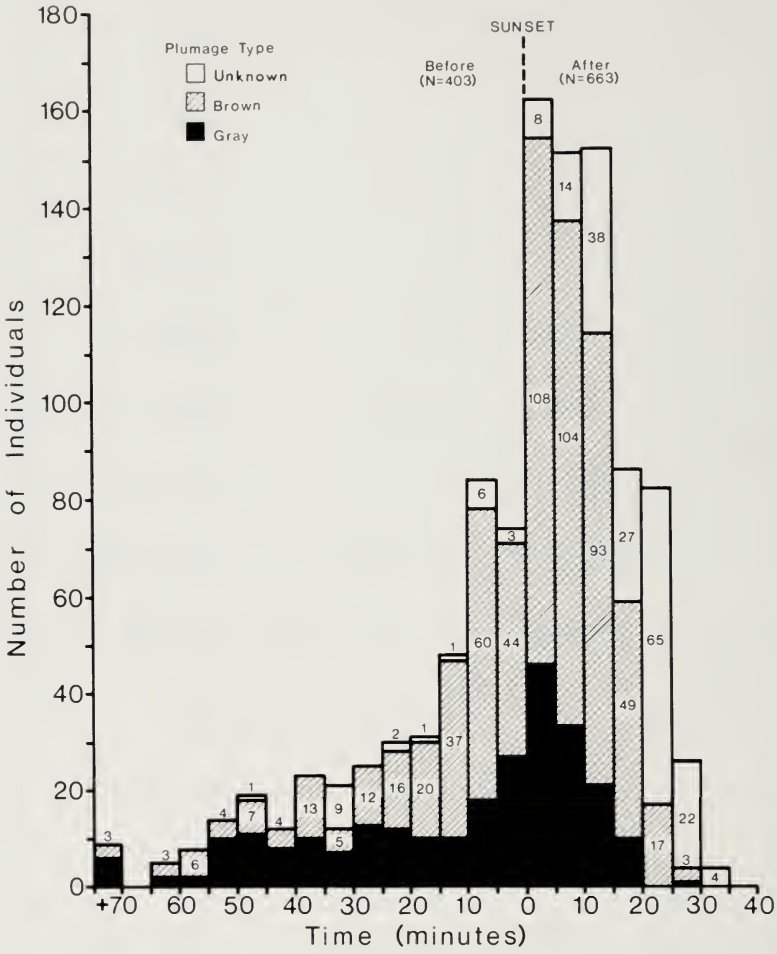

FIG. 7. Number of Snail Kites (N = 1066) arriving at roosts in relation to sunset by 5-min intervals. Numerals above and within the columns are the number of individuals by plumage type.

habitat and new roost sites were used. In 1980 only, kites were found to be roosting singly or in small groups in CA3A. At the same time the number of individuals using two of the larger roosts in CA3A (Nos. 7 and 17) decreased. This probably was a result of some kites that formerly used these roosts shifting to other sites.

The number of birds arriving at the roost before sunset was smaller (37.8%) than those arriving after sunset, and the arrival period was more protracted for early arrivals (Fig. 7). I found gray birds generally went to

roost earlier than brown birds (Mann-Whitney *U*-test, $t_u = 6.57$, $P < 0.001$). A possible reason for this was that brown birds included many immatures which are not as experienced at hunting as older birds and hence took more time to feed in late afternoon.

On cloudy days, when it got dark earlier, kites tended to arrive earlier at roosts, although the difference was not significant (one-tailed test, $t = 1.48$, $P = 0.07$). The mean arrival on cloudy days was 2.6 min before sunset (N = 185, SE = 1.3), as compared to 0.81 min after sunset (N = 673, SE = 0.8) on clear days.

Morning departures from roosts took place over much shorter periods than afternoon arrivals. The mean departure time before sunrise was 15.1 min (N = 13, SE = 1.14), with the earliest bird leaving 22 min before sunrise. The latest that birds left the roost in the morning was 3 min after sunrise. The sample size was insufficient to determine if kites left earlier or later on clear vs cloudy days. Before leaving the roost in the morning kites called, changed perches, made short flights within the roost, or flew around the roost site and returned.

Howell (1932:169) states that, "A colony of kites frequently locates not far from a rookery of herons." In my study I found herons and kites using the same roost sites 81% of the time; overall, 92% of the kite roosts in Florida had other kinds of birds using them, including 12 species of colonial waterbirds and both local species of vultures (Table 2). The three sites that had no other species associates were all extremely small (≤3 kites). The most frequent roost associates were Anhinga (83% of the roosts), Little Blue Heron (72%), Tricolored Heron (67%), and Green-backed Heron (67%). The kites roosted either among or off to the side of other communal birds, but within the same strata. Like kites these other species frequently used the roost sites for nesting.

SUMMARY

A total of 36 roost sites of the Snail Kite (*Rostrhamus sociabilis*) were studied in southern Florida, of which four (11%) were used regularly for 6 or more years. Major roosts were also used as nesting sites. All roosts were in flooded marshes and 33 (91.6%) were in stands of coastal-plain willow. Population increase and the number of roosts were strongly correlated. The number of kites arriving at roosts before sunset was smaller than arriving after sunset (37.8:62.2%), and gray birds (adult and subadult males) generally went to roost earlier than brown birds (all females and immature males). Kites tended to go to roost earlier on cloudy days. Morning departure from roosts was over a much shorter time than arrivals in the afternoon. Ninety-two percent of the kite roosts were also used by other species of birds for roosting, 81% of which were eight species of herons.

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Wilson Bull., 97(1), 1985, pp. 71–77

BEHAVIOR OF YEARLING MALE BLUE GROUSE AND ITS RELATION TO DELAYED BREEDING

Ian G. Jamieson

In species of grouse with dispersed territories, first-year males rarely occupy territories and presumably do not breed (Wiley 1974, Wittenberger 1978). For example, yearling male Blue Grouse (*Dendragapus obscurus*), Ruffed Grouse (*Bonasa umbellus*), and Spruce Grouse (*D. canadensis franklinii*) usually do not defend territories (Bendell and Elliott 1967, Gullion 1967, Herzog and Boag 1978).

Wiley (1974, 1981) and Wittenberger (1978) have proposed separate hypotheses to explain delayed breeding in male grouse. Wittenberger's (1978) sexual selection hypothesis emphasizes inability of yearling males to compete with adults for territories, while Wiley's (1974, 1981) sexual bimaturism hypothesis invokes selection of delayed maturation for males as a consequence of increased early survival and later fecundity.

There have been few detailed studies describing the behavior of yearling male grouse. Important questions about their behavior in regards to the above hypotheses are: (1) do territorial adults actively prevent yearlings from occupying territories and mating with females; and (2) what behavior might enhance early survival and later fecundity? The objectives of this paper are to describe the behavior of yearling male Blue Grouse and to discuss these behaviors in relation to predictions derived from present theories on delayed breeding in grouse.

STUDY AREA AND METHODS

The study area was on Hardwicke Island, off the central-east coast of Vancouver Island, British Columbia. A 460-ha area clear-cut by logging between 1969 and 1973 served as the main study site. Vegetative structure ranged from "very open" (Bendell and Elliott 1967), consisting primarily of burned or unburned slash, mixed grasses, fireweed (*Epilobium angustifolium*), salal (*Gaultheria shallon*), and red huckleberry (*Vaccinium parvifolium*), to "open," consisting mainly of western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) 3–7 m in height.

Trained pointing dogs were used to find birds, which were then captured with a noose pole (Zwickel and Bendell 1967). Selected birds were fitted with either a solar-powered or battery-powered transmitter (Herzog 1979). Birds were captured either in late summer as 2–3 month-old juveniles, or in the following spring as 10–11 month-old yearlings. The transmitter weighed from 2 to 4% of the body weight of the bird and did not appear to affect their behavior.

Observations were conducted in 1980 and 1981 from 14 April, when yearlings first arrived on their summer range, to 22 June. Aggression and spacing behavior are most evident among Blue Grouse during this interval (Jamieson 1983). Observational sessions for individual

birds lasted for at least 1 h and were conducted from after sunrise to darkness. Since I attempted to locate all radio tagged birds during the day as part of the work for other aspects of this study, doing both dawn and dusk observations would not have been feasible. Birds were observed with the aid of binoculars at a mean distance of 20 m (range = 10–80 m), using vegetation as a natural blind. Recording of behavior commenced when the bird appeared undisturbed. Activity was classified as either stationary or moving. A bird was considered to be moving if his position changed more than 1 m in less than 1 min. An interaction was defined as any incident where the behavior of a bird changed in response to the presence of a nearby conspecific. Males were considered territorial if they were highly localized and singing.

RESULTS

Time budget and diurnal activity patterns.—Twenty-four yearling males were watched during 63 and 58 observational sessions in 1980 and 1981, respectively, for a total of 126 h. A median of four sessions (range = 1–14) was conducted on each yearling.

Yearlings were stationary for 74% of the observed time during which they were either inactive (56%) or feeding (18%). Moving occurred 26% of the time and included three activities: feeding (15%), interacting (6%), and walking (5%). At first sighting, birds were in the open, away from vegetative cover, only 30 of the 171 times (18%) that they were located. Individuals located twice in the same day (N = 50) had moved a median distance of 2 m per h (range = 1–24 m).

Percentage of time that yearlings were active (including moving and feeding) ranged from 28% at the 2-h interval around midday to 50% during the 2-h interval before sunset. At dusk, yearlings moved about in the open and sometimes ran 5–15 m in short bursts, or flew short distances of 10–30 m. Twenty-three of the 29 interactions (79%) recorded occurred within 1 h of sunset. In summary, yearlings remained in or near cover and moved very little during the daytime; activity increased at dusk. Yearlings spent approximately one-third of the observed time feeding.

Territorial behavior.—Only one yearling behaved as if on a territory. This bird had stayed in a 0.6-ha area and was heard singing during most of the day for 6 consecutive days. His home range was considerably smaller than that of other yearlings (median = 10.8 ha, range = 0.6–40.7 ha), but similar to that of territorial males (Lewis 1984). In one instance, this male chased away another yearling from his territory. I noted seven other instances of singing by yearlings, two by the same bird; five of these occurred at dusk.

Intraspecific interactions.—Yearling males were observed to encounter territorial males on 25 occasions and each resulted in an agonistic interaction. Adult males that detected yearlings on or near their territories immediately ran or flew toward the yearling and assumed a threat posture

(Jamieson 1984). Yearlings invariably assumed a neutral posture during encounters with territorial males. On 10 occasions they remained in this position for 10–30 sec before flying from the area. In 14 other cases an adult rushed at a yearling and displaced him. I saw only one physical attack in which a territorial male rushed at a yearling and pecked his back, removing several feathers.

In most instances I could not determine what initiated interactions between yearlings and territorial males. However, on at least eight occasions, yearlings made direct movements of 20–250 m towards specific territories where resident males were singing. The movements of the yearlings were conspicuous and once they approached the territories they were chased by the adults in all instances. In all of these cases the yearlings occurred frequently near these particular adults and their territories during the breeding period (Jamieson and Zwickel 1983).

Three yearlings localized near sites that were not occupied by territorial males but which had been occupied the year before. There was no evidence of these males behaving in a territorial manner. One of these birds was resighted the next breeding season and had established a territory where he had localized as a yearling.

Five instances of yearling males interacting with both females and territorial males were observed. In these cases yearlings flew approximately 40–100 m toward females that were calling on or near territories of adult males. They were met immediately by the resident males who courted the females only after they had chased away the yearlings.

Eleven cases in which yearling males interacted with lone females were noted. These interactions were initiated usually in one of two ways; males either walked or flew toward females that had been calling (N = 5), or they encountered them while moving about (N = 5). In one other case a female flew into an area and a yearling responded by flying to where she had landed. On two occasions yearlings did not respond to females that were nearby; both occurred relatively late in the breeding period (4 and 6 June).

Upon approaching a female, yearlings assumed a full or partial display posture and exhibited "head bobbing" (Stirling and Bendell 1970), but did not drag their wings or "whoot" (Stirling and Bendell 1970) as territorial males do during courtship. On three occasions yearlings showed what appeared to be "displacement" behavior by suddenly moving away from the female and pecking at nearby bushes. Yearlings were not observed attempting to mount females as after 1–5 min of displaying they slowly returned to a neutral posture and began feeding. In cases where the responses of the female were monitored, the birds appeared disinterested and either remained still (N = 3) or fed (N = 4). In contrast to yearling males, territorial adult males showed the full range of courtship

responses and attempted frequently to mount females even relatively late in the breeding period when hens were with broods.

DISCUSSION

In promiscuous species of grouse in which territorial males are dispersed, territories presumably allow males to attract, court, and mate with females without interference from other adult males (Bendell and Elliott 1967). Males that localize and perform advertisement behaviors are considered territorial. In my study only 1 of 24 yearling males appeared to be territorial. Instead, yearlings had relatively large home ranges that may encompass several territories of adult males (Jamieson and Zwickel 1983). Also, first-year males are secretive during the daytime and rarely sing. What factors prevent yearlings from occupying territories, thus reducing their chances of breeding? Although testes of yearlings are lighter in weight, develop later, and regress sooner than adults, yearlings produce viable sperm (Hannon et al. 1979) and many will occupy territories and sing if territorial adults are removed (Bendell et al. 1972; Zwickel 1972, 1980). Testes of replacement yearlings are similar in size to those of nonterritorial yearlings (Simard 1964, Zwickel 1980). Therefore, gonadal immaturity does not appear to be sufficient to explain the absence of territorial behavior in yearlings.

Wittenberger (1978) proposed that breeding is delayed in some species of grouse because first-year males cannot compete effectively for territorial sites with older, more experienced adults. My data confirm that adult males can displace yearlings and prevent them from courting females that are on territories of adult males. However, adult male Blue Grouse establish territories 2 weeks before yearling males arrive on the breeding range (F. C. Zwickel, pers. comm.). Therefore, effectively, there is no competition between yearling and adult males for sites. While there may be competition among yearling and older, nonterritorial males for high quality territorial sites when they become available (Jamieson and Zwickel 1983), every year some low quality sites remain vacant on the breeding range (Lewis and Zwickel 1981). A few first-year males localize near these vacant sites, but do not exhibit territorial behavior until their second year. Therefore, inability to compete with adult males is not necessarily a factor in explaining why some yearling males do not behave territorially.

My observations show that yearling male Blue Grouse are sedentary in the daytime, usually feeding in or near vegetative cover. They are most active for short periods at dusk, presumably when potential predators, such as diurnal raptors, are inactive. High activity of yearling males occurs probably at dawn as well (Bendell 1955). In addition, yearlings rarely sing. Although similar data on the time and energy budgets of territorial males

are not available, these males can be heard singing at any time of day and usually from a few specific sites within their territories (Bendell and Elliott 1967, McNicholl 1978). These sites are mainly on open, elevated areas. If territorial behavior increases conspicuousness and vulnerability to predators, as suggested by Wiley (1974), then young, inexperienced birds might have higher mortality rates if they were territorial. Wiley (1974, 1981) argued under the sexual bimaturism hypothesis that yearling males that defer reproduction could be at an advantage if early survival is enhanced. Survival could be increased if time and energy spent in reproductive activities, such as territorial advertisement and maintenance, could instead be allocated to feeding and hiding from predators. Although mortality rates of nonterritorial yearling male Blue Grouse are relatively low (Bendell and Elliott 1967, Lewis and Zwickel 1982), this hypothesis can only be tested by removing territorial adults and then comparing survival rates of replacement yearlings to those of nonterritorial birds. Why do some yearlings take territories if adults are removed? A void of adult males would create an unnatural situation in which the contact rate with receptive females would probably increase as well as allow yearlings to occupy high quality territorial sites.

Some yearling male Blue Grouse associate with a few territories occupied by adult males (Jamieson and Zwickel 1983) and appear to initiate interactions with territorial males on these sites. Similarly, yearling male Spruce Grouse seemed to be attracted to sites of advertising males and some made flights of unknown motivation onto territories where they were immediately displaced by the resident male (Nugent 1979). Territories of Blue Grouse differ in quality as males on some sites have higher survival and better chances to breed than males on other sites (Lewis and Zwickel 1981). Males that do not occupy territories as yearlings, but instead localize near high quality sites, may increase their chances of securing one of these sites once they become available (Jamieson and Zwickel 1983). This agrees with Wiley's (1974, 1981) suggestion that deferment of reproductive activity may result in increased fecundity at a later age.

Finally, I wanted to know if adult males could inhibit yearlings from attempting to mate with females. Wiley (1981) remarks that even when an optimal life history pattern involves a deferment of reproductive activities at early ages, an individual should not pass up opportunities to breed if risk and effort are low. Adult Blue Grouse displaced yearlings that had intruded onto territories to court females, but yearlings also displayed to females encountered away from territories of adult males. Yet, in these cases, they did not express the full range of courtship responses shown by territorial males. Furthermore, they did not attempt to

copulate and, in some cases, quickly became disinterested in the females. There may be several proximate factors affecting the mating behavior of yearlings. These factors include: (1) the full range of courtship behaviors may not have been developed or learned (see Kruijt and Hogan 1967: 234); (2) females may have to show receptive postures before yearlings become motivated to elicit mating responses; or (3) a territory must be acquired before yearlings show mating behaviors similar to adults. In removal experiments, replacement yearlings sang, occupied territories, and presumably bred (Bendell et al. 1972; Zwickel 1972, 1980). However, no observational data were published on their mating behavior.

Inability of yearling male Blue Grouse to compete for territories with adult males does not explain why some yearlings do not behave territorially on unoccupied sites. Sedentary or secretive behavior of yearlings coupled with associating with high quality territorial sites could conceivably enhance early survival and later fecundity as proposed by Wiley (1974, 1981), but this has yet to be tested. Failure of yearlings to attempt to copulate with females suggests that more emphasis is needed on proximate causes and development of mating behaviors in order to derive a better understanding of the phenomenon of delayed breeding.

SUMMARY

Yearling male Blue Grouse (*Dendragapus obscurus*) were inactive during the day and were usually in or near vegetative cover; overt activity increased at dusk. Adult males displaced yearling intruders from their territories. However, some yearling males appeared to initiate agonistic interactions with territorial males. Other yearlings localized near unoccupied territorial sites but did not behave territorially. Yearlings displayed to, and courted, females away from territories of adult males but did not show the full range of courtship behaviors given by territorial males, and made no attempt to copulate. Results partially support predictions on behavior of yearling males derived from the sexual bimaturism hypothesis to explain why first-year males of most promiscuous species of grouse delay breeding.

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BROOD CHRONOLOGY OF THE COMMON RAVEN

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The Common Raven (*Corvus corax*) is a widely distributed Holarctic species (Goodwin 1976). This corvid occurs over most of the western United States (Good 1952), but is common only in restricted, often remote locations (Bent 1962).

Aside from the descriptions of nest construction by Kulczycki (1973), behavior of captive ravens (e.g., Gwinner 1965), and the observational reports by Kochert et al. (1976, 1977), few investigations have been published that describe the nesting chronology and reproductive biology of a large population of free-flying ravens. The study reported herein was undertaken as a part of a larger investigation (Stiehl 1978) and describes the nesting chronology and reproductive success of a population of Common Ravens in southeastern Oregon.

STUDY AREA AND METHODS

Field work was conducted near Malheur National Wildlife Refuge, located in Harney County, Oregon. This large area (73,250 ha) has an average elevation of 1350 m. The major land forms consist of alkaline lake and marshland covering 32,400 ha, river valley uplands supporting *Carex* and other submerged and emergent plants, and extensive rimrock areas of volcanic and fault block origin. On the plateaus of the surrounding area above the rimrocks, typical Great Basin desert vegetation of sagebrush (*Artemesia* sp.) and greasewood (*Sarcobatus* sp.) form the dominant communities. The extensive rimrock formations provide locations for nest-sites and the vast wetland provides a food base for a nesting population of 40–50 pairs of ravens.

In 1975, potential nest-sites were located by systematically searching rimrocks, suitable trees, and deserted buildings during the nesting season. As a nest was found, the location was plotted on a map and the site marked with plastic flagging. In 1976 and 1977, each nest was inspected at least once within each 7-day period throughout the nesting season. I used an auto mirror attached to a 1.5-m length of soft copper tubing similar to that used by Rowley (1973) to inspect nest contents where direct observation was not possible.

RESULTS

Nest location.—During the study I observed a total of 87 active Common Raven nests. Forty-five nests were found in 1976 and 42 nests in 1977. The nest density was $\frac{1}{22}$ km^2 for the 32 nests on the refuge in 1976 and $\frac{1}{25.2}$ km^2 for 29 nests in 1977. The nesting density was lower for nests off the refuge, but could not be calculated accurately as nests were scattered in the patchy habitat. Most nests (74%, N = 64) were situated on rimrocks. Abandoned buildings and windmills accounted for 23% (N = 20) of the nest-sites and three nests were located in trees (western juniper [*Juniperus occidentalis*] and willow [*Salex* sp.]).

Regardless of substrate, 49% (N = 43) of the nests were used for both of the years of study. Refuge personnel stated that several nests had been active for at least 6 years at the same location. No physical conflict for nest-sites was observed during the study, but Great Horned Owls (*Bubo virginianus*), Red-tailed Hawks (*Buteo jamaicensis*) and Golden Eagles (*Aquila chrysaetos*) nested in the same habitats in the area. A nest used by Golden Eagles and another used by Great Horned Owls in 1976 were used by ravens in 1977. Two nests, which ravens used in 1976, were used by Great Horned Owls in 1977. Prior to my study, a nest built by ravens was used by ravens, Red-tailed Hawks, and Great Horned Owls in 3 consecutive years (John Scharff, pers. comm.).

There appeared to be no relationship between the success (fledging of one or more young) of the nesting attempt and the reuse of the same nest the following nesting season. I used differences in aggressive behavior as I approached the nest (Knight 1984), and peculiarities in vocal patterns (Brown 1974) to identify eight nesting pairs of ravens. Of this group, four pairs used the same nest, after some reconstruction and repair, in both 1976 and 1977. Two pairs built a new nest and attempted to renest the same year after nest failure and two pairs changed nest location in 1977 after successfully nesting in 1976.

Nest construction.—Nest construction that I observed (N = 17) resembled that reported by Kulczycki (1973). After a territory was established in late February (Stiehl 1981), both partners participated in nest construction or repair. Sagebrush and greasewood were placed and woven until a large basket (20 cm × 40 cm diameter) lined with cattle hair, shredded juniper bark, and grasses was formed (Fig. 1). I observed both members carrying these materials to the nest site, but only noted the female actually building the basket.

Although the average diameter of 46 nests was 40.5 ± 4.5 cm, this dimension seemed to be related to the type of substrate used. Nests on rimrock ledges usually filled the space available. Nests in buildings and trees were generally larger than rimrock nests.

Normal compacting of the nest by the chicks and adults, and fouling of the nest by the chicks, as well as seasonal deterioration, necessitated reconstruction prior to reuse. Reconstruction was also observed when the same nest was used twice in the same nesting season, after failure of the first clutch (N = 4), even though the nest appeared to be structurally sound. The reconstruction was similar to new construction; however, no new soil was added to the existing structure.

Egg-laying and incubation.—Egg-laying began in early March. Exact dates were established based on visual inspection on at least 2 consecutive

FIG. 1. A typical rimrock nest of a Common Raven. The nest is about 4 m above the ground.

TABLE 1
NESTING PHENOLOGY FOR *CORVUS CORAX*, MALHEUR NWR, 1976–77

Period	No. of nests with		
	Eggs	Hatchlings	Fledglings
7–15 March	8	0	0
16–31 March	15	4	0
1–15 April	24	16	0
16–30 April	12	20	0
1–15 May	11	10	8
16–31 May	1	8	18
1–15 June	0	2	11
16–31 June	0	0	8
1–7 July	0	0	4
Exact period unknown	0	0	4
Total	71	60	53

days, with at least 1 day when no eggs were present, or calculated on the hatching or fledging dates of birds in a particular nest. Using both of these methods, the median laying date for both years was 4 April and egg-laying occurred from 7 March to 16 May (Table 1). The median includes some known second and third clutches.

In 14 observations of the complete egg-laying sequence, a 24-h delay followed the laying of the first egg. After this, eggs were layed at about 24-h intervals until the clutch was complete. Based on observations of hatching sequence (N = 12), I determined that incubation began with the second egg laid, contrary to the reports of Gwinner (1965) and Goodwin (1976) but in agreement with Holyoak (1967). For the population I studied, the incubation period was 20.9 ± 1.16 days for 36 nests. The mean clutch-size for 19 nests was 5.8 (SD = ±1.1) in 1976 and was 6.1 (SD = ±0.8) for 26 nests in 1977. Ratcliffe (1962) reported a mean clutch-size of 4.6, whereas Holyoak (1967) gives 5.2 as a mean clutch-size. Kochert et al. (1976) reported a mean of 5.2 eggs (N = 10) for ravens nesting in southwestern Idaho in 1976, and 5.38 (N = 21) in the following year (Kochert et al. 1977). Holyoak (1967) suggests that the clutch-size varies from 3 to 6 eggs. Goodwin (1976) also states ravens lay from 3 to 6 eggs, rarely fewer than 3 and very rarely 7 eggs. During this study, the clutch-size of 45 nests could be accurately determined. Fifteen nests (33%) were found with a complete clutch of 7 eggs. The differences in clutch-size may be attributed to more abundant food sources in my study area or perhaps an adaptation to optimum survivorship as suggested by Lack (1954).

I only saw females incubating eggs, but males provided food for females during incubation. I recorded 23 such feedings of two basic types. As the male approached the nest, direct feeding was initiated by quivering (Goodwin 1976) and "*koww*" calls (Brown 1974) by the female. Food was then regurgitated by the male in a manner typical of chick feeding. If the female did not vocalize, the food was placed on the nest rim or within 2 m of the nest by the male. When near the nest, the male would "stand guard" (cf. Bent 1962) in a prominent location with a commanding view of the area, but direct view of the nest did not appear to be critical.

The nest was occasionally unattended when the female left for short (ca. 10 min) periods. The frequency of these flights increased from two per 10-h period early in incubation to five in an 8-h period during the latter stages of incubation. The purpose of these flights was not determined.

Females left the nest to assist their mate in nest defense against other ravens (N = 6), Red-tailed Hawks (N = 2), and Golden Eagles (N = 1). In all cases, the female joined the male after he began his pursuit and she returned before the male returned to the nest.

Hatching.—Normally one of the eggs failed to hatch (cf. Goodwin 1976). Unhatched eggs remained in the nest from 4 to 7 days after the other eggs hatched. The fate of an unhatched egg was not determined in this study, but Holyoak (1967) states that brood parents consume it within 12 days. I analyzed over 1100 regurgitated pellets and found raven egg shell in five. These shells, however, may have been from either hatched or unhatched eggs, or perhaps depredated eggs from other nests.

The average brood-size for 1976 was 4.0 ± 1.6 (N = 25) and for 1977 was 4.4 ± 1.8 (N = 26). Kochert et al. (1976, 1977) reports average brood sizes of 3.66 (N = 21) and 3.09 (N = 22). For nests with both clutch-size and brood numbers known (N = 41), 69% of the eggs hatched in 1976 and 71% hatched in 1977.

I could not elicit chick begging until 3 days post hatch, indicating that audition did not function at hatch, that sound recognition required several days to develop, or that chicks were not physically able to beg at an earlier age. At 6 days post hatch, vocalizations accompanied the begging. Dorsal pterylae were first visible as a grey band at 5–6 days. Eyes opened between 12 and 14 days post hatch. The development of sight accompanied a major behavioral change in the chicks. Between 6 and 14 days post hatch, I could easily elicit begging and vocalizations. After the eyes opened, the 14-day-old chicks crouched low in the nest and remained silent at my approach. If the reaction were similar to potential nest predators, then locating the nest could have been facilitated by the vocalizations of the chicks. As 71% (N = 12) of the nest depredations occurred between hatch

and 14 days post hatch, the development of sight appeared to be critical to nesting success. No predators were observed, but signs at the nests suggested coyote (*Canis latrans*), raccoon (*Procyon lotor*), weasel (*Mustela* sp.), Great Horned Owl, and man. I was often harassed by the adults during nest inspections, but the defense would not have been sufficient to effectively deter most mammalian predators.

Renesting.—Neither the depredation of eggs nor hatchlings necessarily precluded reproductive success of the nesting pair. Six pairs laid replacement clutches following destruction of the eggs or chicks. Additionally, based on normal dates of nesting, two other pairs laid replacement clutches during the study. One pair renested three times in the 1976 season, and another renested after the loss of both the female parent and the brood. The brood was destroyed at about 16 days post hatch. The female had been shot and was found dead near the nest. There was another set of eggs in the nest. The male had remated and, using the same nest, the new pair successfully reared a brood.

The ability to lay replacement clutches has been reported in many species, including some corvids. Took (1937) reported renesting in Carrion Crows (*C. corone*) and Rowley (1973) reported clutch replacement in the Little Raven (*C. mellori*). Bowles and Decker (1930) noted replacement clutches in *C. corax* after egg predation. Laying replacement clutches after loss of chicks has not, to my knowledge, been reported previously for Common Ravens. Nest loss did not always result in another nesting attempt. Although there were six depredations of nests with eggs or chicks after 5 May, I recorded only three renesting attempts after that date. After a nesting failure, nest construction efforts were accelerated and resulted in a period as short as 11 days between loss and completion of a replacement clutch. Initial nesting attempts required 14–20 days, suggesting that some time is required for initial territorial establishment. After nest loss, I observed either reuse of the same nest (N = 4) after some reconstruction, or building and use of a new nest (N = 2) within 100 m of the old nest. The same nesting substrate was used in 5 of the 6 cases.

Fledging.—For 122 nestlings of known age in my population, fledging started at 41 days (±3) post hatch. Higher precision is impossible due to asynchronous hatch. Sustained flight is not possible for young ravens even after fledging. Young forced from the nest at 35–45 days post hatch glide up to 150 m from the nest and then hop back to the nest. Short flights were characterized by very rapid wing beats and an extended recovery period, during which panting was observed and frequent distress calls were heard.

The mean fledging success was 2.2 (SD = ±2.1) for 25 nests in 1976 and 2.5 (SD = ±2.0) for 28 nests in 1977 (Table 2). Kochert et al. (1976)

TABLE 2
NESTING SUCCESS FOR *CORVUS CORAX*, MALHEUR NWR, OREGON, 1976–77

	1976		1977		All years	
	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD
Eggs	19	5.8 ± 1.1	26	6.1 ± 0.8	45	6.0 ± 0.9
Hatch	25	4.0 ± 1.6	26	4.4 ± 1.8	51	4.2 ± 1.7
Fledged	25	2.2 ± 2.1	28	2.5 ± 2.0	53	2.3 ± 2.0

reports similar success for the same period. Of the 85 nesting attempts observed during the study, 51 (60%) were successful in fledging one or more young. Hooper et al. (1975) reported 63% nest success, whereas Allin (1968) reported 80% success. Dorn (1972) reported 58% success. Factors that decreased fledging success in this study included depredation (N = 20 nests), starvation (N = 7 nests), human disturbance (N = 5 nests), and falling from the nesting substrate (N = 2 nests). Considering these losses, 74% (N = 90) of the hatched young subsequently fledged during the study period.

Examination and palpation of 71 dead nestlings indicated that starvation was the probable cause of death for 16 nestlings (22% of total nestling death [N = 71]) in 1976 and 34 (33% of total nestling death [N = 103]) in 1977. The higher percentage in 1977 coincided with a drought which delayed peak waterfowl nesting about 14 days, whereas the raven nesting period was the same for both years. Avian eggs (principally waterfowl) formed a high proportion of the diet for 13 of the 25 nesting pairs in which starvation occurred. This suggests that a delayed waterfowl nesting season may have accounted for the higher starvation rate in 1977, and may reinforce the suggestion that asynchronous hatch is an adaptation to variations in food availability as suggested by Lack (1947) and Lockie (1955).

I noted two different behavior patterns of the fledglings that appeared to be associated with the date of fledging. Due to nest destruction and predation, the fledging period extended from 8 May to 7 July (Table 1). The ravens that fledged early in the season (8 May–25 May) were presumed to be from successful first nesting attempts. All successful renesting attempts I recorded resulted in fledging after 1 June. Therefore if fledging occurred after 1 June, the first nesting attempt was presumed to have failed.

Behavior of young fledged early in the nesting season.—The young that fledged early in the season (before 25 May) were observed in the vicinity

of the nest for up to 6 weeks after they were seen flying for short distances. During this period, although the fledglings became adept at flying, the adults continued to provide food for them. Both adults fed the young. Upon arrival of an adult, all fledglings directed their attention toward that adult, even if the returning bird did not have food. The young hopped or flew to the adults and begged intensively. One to three young were fed by adults upon arrival, although some young were fed more frequently than others. The probability of being fed at a particular time appeared to be related to begging intensity, however, all young were fed at least once during each of my 4-h observation periods (N = 8) at five nests. Food was either regurgitated directly into the gaping mouths or placed on the ground near the larger fledglings. Up to 4 or 5 weeks post hatch, the young were never observed more than 200 m from the nest, perched either on the rimrock (rimrock nests), buildings or other structures (structure nests), or nearby trees and shrubs (tree nests). From these sites, the fledglings made short flights which resulted in 10–15-m vertical drops. The flight by the first fledgling to depart was then mimicked by the rest of the brood.

After 4–5 weeks (65–78 days post hatch) the young accompanied the adults on flights, but the nest-site remained the center of activity. Due to the terrain, the purpose and extent of these flights were not determined. Typically both adults accompanied the brood on these flights. I suspect that the main purpose of these flights was feeding, and that such family flights possibly play an important role in the formation of food preferences in the young. Early morning and late evening observations indicated that the nest-site was used as a roost by the family until the group left the area.

Behavior of young fledging late in the nesting season.—Young that fledged late in the season, probably because of failure of an earlier nesting attempt, displayed behaviors similar to those just described, except that the period of "nest-centered" behavior was compressed. The fledglings remained near the nest for only 5–7 days, and followed the adults for short distances (500 m) as early as 50 days post hatch. Observations of young 500–800 m from the nest were not uncommon for the young which fledged late in the season. I observed less "practice" flying, and although the fledglings did not appear to develop flight skills any faster than early fledged young, they attempted to follow the adults at 10–14 days after fledging (47–54 days post hatch).

The differences in the behavior of fledglings appeared to be related to changes in food preference or availability that occurred in July. The diets of ravens shifted from carrion, small mammals, and eggs to insects, principally grasshoppers (Orthoptera), at that time. Although the availability of small mammals (based on trapping success) and carrion was unchanged,

fewer eggs were available. Ravens were noted more often feeding in areas that had large populations of grasshoppers. In response to the change in the diet, family groups spent more time away from the nest-sites, gathered into increasingly larger flocks, and emigrated from the study area. I saw large flocks of ravens feeding on grasshoppers in cultivated fields up to 100 km from the study area in August of both study years.

Hatchling anomalies.—A total of 214 hatchling ravens from 51 nests were recorded in the study. Of these, seven birds (3.3%) from three nests had detectable anomalies. As no tissues were collected for analysis, the cause of these anomalies could not be determined.

Five ravens, all from the same nest, had gross foot deformities that prevented perching and grasping of food. Ravens often hold down their food in one or both feet as it is eaten. The dead young appeared to have died from either exposure (1 case) or starvation (4 cases). Although the starvation was a result of the foot deformities, it was probably facilitated when the adults deserted the young after the first fledgling died.

Two hatchlings, from separate nests, had malformed beaks. Both were found dead near the nest and were estimated to be from 20 to 25 days old. Other siblings did not appear deformed, and as the adults did not appear to alter their feeding patterns, the other young of the broods (three and two birds, respectively) may have benefited, through increased feeding by the adults, from the death of the deformed hatchling.

SUMMARY

Brood chronology and nesting success of the Common Raven (*Corvus corax*) were studied during 1976 and 1977 nesting seasons on Malheur National Wildlife Refuge in southeastern Oregon. Nest construction or reconstruction began in late February and early March. Egg-laying began during the second week of March and continued through early May. Peak egg-laying occurred the first week of April. In 1976 the mean clutch-size was 5.8 eggs/clutch (N = 19) and in 1977 was 6.1 eggs/clutch (N = 26). The incubation period was about 21 days. Hatching success was 4.0 eggs/clutch in 1976 (N = 25) and 4.4 eggs/clutch in 1977 (N = 26). Productivity was 2.2 young/nest in 1976 (N = 25) and 2.5 young/nest in 1977 (N = 28). Predation on and starvation of nestlings were the primary reasons for the low productivity/clutch-size ratio. Renesting after egg destruction was observed on seven occasions with renesting after predation of hatchlings observed four times in the study. Productivity and renesting after hatchling destruction have not been reported previously in natural populations of Common Ravens.

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ON ATMOSPHERIC MOISTURE AS A FACTOR INFLUENCING DISTRIBUTION OF BREEDING BIRDS IN TEMPERATE DECIDUOUS FOREST

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Vegetation structure, frequently measured as "foliage height diversity" (FHD; MacArthur and MacArthur 1961), has been shown to be correlated with bird species diversity across seral stages of vegetation (e.g., MacArthur 1964, Karr 1968, Recher 1969) and within seral stages of geographical and structural similarity (e.g., MacArthur and MacArthur 1961, MacArthur 1964). However, the validity of the correlation within similarly structured habitats has been questioned (e.g., Tomoff 1974, Wiens 1974, Willson 1974). Willson (1974) and Roth (1976) contend that there is a need for a heterogeneity index that is sensitive to both subtle and large-scale variation in vegetation structure. Although there have been several attempts to develop a universal predictor of species diversity (see Roth 1976), they have met with limited success. MacArthur (1964) and Rotenberry and Wiens (1980) theorized that birds in desert scrub were selecting habitat in response to factors other than foliage structure.

MacArthur and Wilson (1967) postulated that the incorporation of additional environmental variables would increase the accuracy of a biotic diversity index. One of these variables could be atmospheric moisture. The significance of relative humidity for the behavior and physiology of many terrestrial animals has been well documented. Whittaker (1952) and Janzen and Schoener (1968) found total insect densities to be correlated with stand moisture. Janzen and Schoener (1968) related intraforest moisture to insect species diversity, indicating the importance of this environmental constituent in the distribution of arthropods.

Several studies have shown that abundance of breeding birds increases from xeric to mesic woodlands (e.g., Odum 1950, Smith 1977). Kendeigh and Fawver (1981) considered the changes in bird species within a particular stand as possibly a response to moisture. Stamp (1978) suggested that food resources may influence the relationship between FHD and avian community structure, and that "future studies should also investigate climatic variables as estimators of resource variation . . . ." Bertin (1977) demonstrated that soil moisture is a necessary component in habitat selection of two woodland thrushes, *Catharus fuscescens* and *Hylocichla mustelina*, and that "factors such as moisture regime or postulated microclimate variables may be more highly correlated than vegetation structure with abundances of certain bird species." More recently, Swift

et al. (1984) found significant correlations between measures of soil moisture and avian community parameters.

The purpose of this study was to measure structural heterogeneity and relative humidity in samples of mature deciduous forest and to determine whether these factors were correlated with the species diversity of birds breeding there.

METHODS

The 20 sites chosen for this study are located in Portage, Summit, and Wayne counties in northeastern Ohio. We classified the climax vegetation type in each of the study plots as beech-maple, oak-hickory, or mixed mesophytic deciduous forest (Table 1). The majority of the plots contained red oak (*Quercus rubra*), white oak (*Q. alba*), American beech (*Fagus americana*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), shagbark hickory (*Carya ovata*), and white ash (*Fraxinus americana*).

Records were collected on the 20 sites between 15 June and 1 August 1980. Each site was situated within a mature deciduous woodland that included trees approximately 20 m in height, and a closed canopy. Each plot encompassed 0.8 ha, a small area in comparison to most studies of this type. However, in order to ensure a relatively constant microclimate (i.e., relative humidity) on each site, 0.8-ha plots were necessary. No site had a boundary with other than an extension of the mature forest, so any edge effect resulting from borders with open fields or other "younger" successional growth was eliminated.

Foliage density was measured using the method of MacArthur and MacArthur (1961). A series of heights above the ground was used to construct a profile of foliage density plotted against height of vegetation. The vertical width of the density board was 1 m, and was centered on four heights that generally corresponded to herb (0.6 m), shrub (1.8 m and 3.6 m), and understory (7.0 m) layers. All canopies were closed (70%–85% cover) and were not included in the analysis because they were considered to be homogeneous. Both Karr and Roth (1971) and Willson (1974) give evidence that the mere existence of the canopy layer is sufficient to increase avian community composition. Further additions to canopy foliage volume (over 50% cover; Willson 1974) did not increase the number of species present. Foliage density was expressed in units of leaf area per unit volume (m^2/m^3). Foliage density was measured for each height at three random locations in each study area. The values were averaged to give a single foliage density estimate at each of the four heights.

To separate mesic woodlands from xeric woodlands quantitatively, two hygrometers were used simultaneously. One was placed in the study plot 1.5–2.0 m above the ground, and at least 0.5 m away from any foliage, and the other was read in a shadow at a similar height in a nearby open area outside the woodland. The readings for each plot were taken on three different days (between 10:00 and 13:00); rainy weather was avoided. The average percent difference in relative humidity between inside and outside the woodland was employed as the atmospheric moisture index for each woodland. Typically, moisture gradients are based on topographic position and plant species present (Whittaker 1960, Smith 1977). By measuring these two parameters, a general index of the moisture regime can be estimated across large tracts of land. This index would be unsuitable, however, for resolving smaller variations in moisture, as was necessary in the present study. Although slope direction proved to be a reliable indicator, the hygrometric technique provided a more detailed, quantitative estimate of ambient moisture.

The direction (N, NE, E, etc.) faced by sloping areas was recorded with no distinctions made to the degree (angle) of the slope; none of the slopes was very steep.

TABLE 1

FOREST TYPE, RELATIVE HUMIDITY VALUE, FOLIAGE HEIGHT DIVERSITY, SLOPE DIRECTION AND BIRD SPECIES RICHNESS FOR EACH OF THE 20 OHIO STUDY PLOTS ARRANGED FROM HIGHEST TO LOWEST RELATIVE HUMIDITY INDEX

Study plot	Forest type	Relative humidity value (%)	Foliage height diversity	Slope direction	Number of species of birds
12	Beech-maple	28.7	1.36	NW	14
10	Beech-maple	28.7	1.33	No slope	13
15	Mixed mesophytic	26.8	1.23	No slope	15
17	Oak-hickory	25.3	0.98	E	15
11	Beech-maple	24.8	1.23	No slope	11
1	Mixed mesophytic	24.6	1.13	NE	12
14	Mixed mesophytic	21.7	0.88	NW	5
3	Mixed mesophytic	21.1	1.36	N	10
16	Oak-hickory	20.3	1.34	NW	5
4	Mixed mesophytic	18.6	1.35	NW	9
7	Mixed mesophytic	18.5	1.34	SW	9
6	Mixed mesophytic	17.2	1.19	W	3
13	Mixed mesophytic	16.4	1.18	W	9
5	Mixed mesophytic	16.3	1.31	SW	9
18	Mixed mesophytic	14.5	1.13	SW	12
20	Oak-hickory	14.2	0.08	W	8
2	Mixed mesophytic	11.9	1.26	SW	10
9	Mixed mesophytic	11.3	1.25	W	7
8	Mixed mesophytic	10.1	0.67	SW	8
19	Mixed mesophytic	9.6	1.28	W	9

Birds were censused by a single observer who walked along two parallel transects. Birds seen or heard were counted only if they were within 22 m of the transect route. Each of the 20 plots was censused once on each of 3 or 4 days. Each census took 30–40 min and occurred between 08:00 and 10:00. Because the area of each sample plot was small, mapping actual territories of the breeding birds was not practical. Our census results, therefore, indicate the relative use of each site by foraging birds.

We used the Shannon-Wiener Diversity Index (H') to describe the complexity of foliage in each plot. Foliage height diversity was calculated,

$$H' = -\Sigma\, p_i \log_e p_i,$$

where p_i is the proportion of the total foliage volume that occurs in the ith horizontal layer. High estimates of FHD suggest generally uniform density of vegetation in most or all of the four height intervals. Both the number of individuals and the number of species censused were used to quantify avian use of each site.

RESULTS

Indices of relative humidity characterizing a woodland ranged from 9.6% to 28.7% (Table 1). Total foliage density ranged from 0.032 m^2/m^3

TABLE 2
PEARSON CORRELATIONS (R) BETWEEN PAIRS OF VARIABLES

Variable	Number of species of birds	Number of individual birds	Moisture index
Moisture index	0.543[a]	−0.057	—
Foliage height diversity	−0.195	−0.215	0.266
Total foliage density	0.464[a]	0.349	0.618[a]
Foliage density (0.6 m)	0.431	0.348	0.483[a]
Foliage density (1.8 m)	0.158	0.088	0.452[a]
Foliage density (3.6 m)	−0.048	0.266	0.600[a]
Foliage density (7.0 m)	0.386	0.216	0.359
Foliage density (0.6 m + 1.8 m)	0.409	0.313	—
Foliage density (1.8 m + 3.6 m)	0.292	0.159	—
Foliage density (3.6 m + 7.0 m)	0.497[a]	0.271	—

[a] Significant at $P < 0.05$.

to 0.764 m^2/m^3. Several significant relationships were demonstrated between avian community structure and environmental variables (Table 2). The total number of birds did not increase in the more moist situations ($r = -0.057$; $P > 0.50$). The number of species, however, increased from xeric to mesic woodlands ($r = 0.543$; $P < 0.05$; Fig. 1). Total foliage density and foliage density in the combined upper shrub and understory layers were also correlated to the number of species on each plot ($r = 0.464$ and $r = 0.497$, respectively; both $P < 0.05$), but FHD did not have a significant correlation with the number of bird species ($r = -0.195$; $P > 0.50$). Relative humidity was correlated significantly with overall foliage density ($r = 0.618$; $P < 0.01$), and with foliage density of each layer of vegetation except the 7.0 m layer. We used partial correlation analysis (Steel and Torrie 1980) to clarify the relationship between number of species on each plot and its influencing factor. This statistic measures the strength of the relationship between number of species on each plot and one of the independent variables with the other independent variable held constant. Relative humidity ($r = 0.530$; $P < 0.02$) was more highly correlated with number of species on each plot, with foliage density held constant, than was foliage density ($r = 0.196$; $P > 0.10$), with relative humidity held constant.

The direction the ground in the woodland sloped was highly related to woodland atmospheric moisture (median test; $P < 0.001$). The 10 woodlands with the higher moisture values faced north, northwest, or had no slope, while the remaining 10 study areas faced south, southwest, or west.

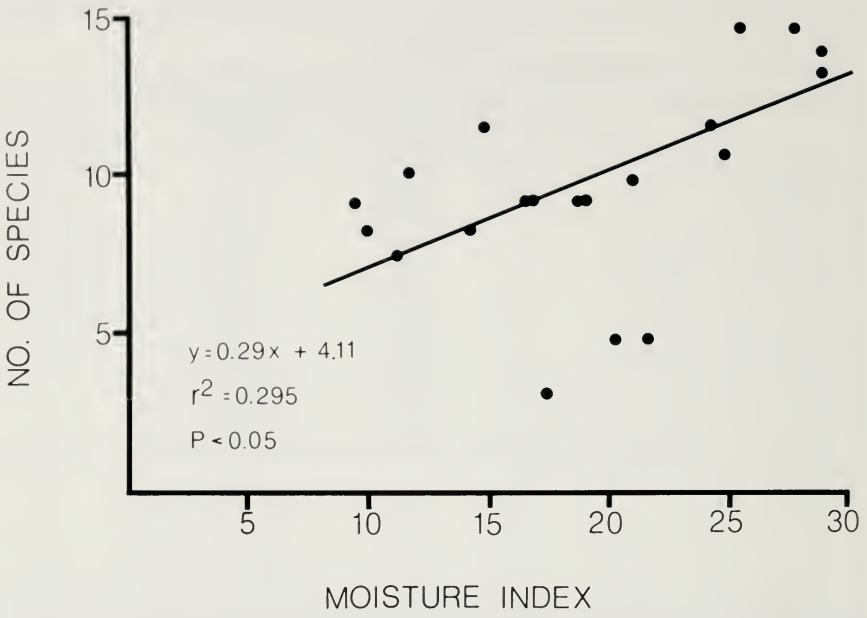

FIG. 1. Scatter diagram and regression line for correlation between bird species richness and the moisture index.

DISCUSSION

That species richness and foliage density were significantly related only at the combined 3.6 m and 7.0 m level may be a consequence of the disproportionately large number of species that use this layer. Approximately three-fourths of the species censused nest in and/or forage to a large extent in the 3.6–7.0 m zone of vegetation. Unlike MacArthur and MacArthur (1961), we do not feel that all layers of vegetation (determined by the observer) are equally important in regulating avian community structure. An "imbalance" in avian community composition favoring certain height intervals may escalate the importance of these vegetative layers.

The suggestion by Willson (1974) and Roth (1976) that the FHD index is unsuitable for similarly structured habitats appears to be true in this study. This does not imply, however, that a more sensitive heterogeneity index would escalate the accuracy of such a predictor of avian community structure in similar habitats. Once habitats obtain a certain similarity, slight contrasts in foliage structure may no longer regulate species composition. In other words, the niche-gestalt (James 1971) of a species be-

comes satisfied and one or more additional factors may influence microhabitat selection (Wiens and Rotenberry 1981).

Foliage is of main importance to most woodland bird species for nesting, feeding, and protection from predators. Once suitable habitat is located, avian populations should tend to favor those areas that contain the most abundant food resources. Relative humidity may be significant to birds because of its effects on food resources. Atmospheric moisture is an essential component of terrestrial arthropod development, growth, and metabolic activity (Neville 1975, Horn 1976, Edney 1977). As all bird species in our study were predominantly insectivorous, especially when feeding young, it seems probable that the avian community would respond to the more abundant food resources in the moister areas. Other studies (e.g., Odum 1950, Murray 1954, Bond 1957) have shown total avian populations to be correlated with forest moisture. Whittaker (1952) demonstrated a greater insect abundance with increasing moisture in different woodland types. This indicates that the correlation with avian species richness may be directly with food supply and only indirectly with the moisture regime. Alternatively, Karr and Freemark (1983) speculated that a tropical avian community responded to a moisture gradient for physiological reasons. As this hypothesis lacks definitive evidence, it would be difficult to assess physiological stress as a cause for the response to the moisture gradient in our study.

We suggest that the bird species that "entered" a habitat only when a certain threshold was reached were those species dependent on food sources intimately associated with moisture. Of the 23 species censused during the study, the Red-bellied Woodpecker (*Melanerpes carolinus*) and Hairy Woodpecker (*Picoides villosus*), both of which dig for arthropods in decaying wood, displayed the most profound preference for high humidity conditions. Two of five other species showing a strong affinity for high moisture areas, the Wood Thrush (*Hylocichla mustelina*) and Ovenbird (*Seiurus aurocapillus*), are both ground-litter foragers. The Hooded Warbler (*Wilsonia citrina*), the fifth most moisture-preferring species, also forages in leaf litter (Bent 1953). All five species were uncommon on the study plots, thereby accounting for the lack of correlation between moisture and number of individuals foraging on each site.

The moisture content of both leaf litter and dead or dying trunks and branches is substantially determined by the ambient humidity (Strickland 1947, Larkin and Elbourn 1964). As ambient humidity increases, arthropod abundances escalate in leaf litter (Strickland 1947, Jaeger 1972, Plowman 1979) and in dead trunks and branches (Larkin and Elbourn 1964, Elbourn 1970). The relationship with atmospheric moisture of the five bird species mentioned above may have been directly in response to the

augmented abundances of arthropods in their specific foraging substrates. Bertin (1977) suggested that bird species most sensitive to soil moisture would be ground foragers.

There were no other leaf-litter foragers, except for the American Robin (*Turdus migratorius*), which forages in short grass in open country. The other trunk foragers, Northern Flicker (*Colaptes auratus*), Downy Woodpecker (*Picoides pubescens*), and White-breasted Nuthatch (*Sitta carolinensis*), do not excavate dead wood to the extent Red-bellied and Hairy woodpeckers do. The Downy Woodpecker often selects foraging sites with a high density of saplings (Anderson and Shugart 1974, pers. obs.). Downy Woodpeckers can exploit a wide array of foraging substrates, and therefore, do not show a preference for moist habitats (Bond 1957, Smith 1977, this study). Their reliance on dead wood as a food matrix is not as great as the reliance of larger woodpeckers because food resources are available on small branches, larger herbaceous plants, and other substrates that Red-bellied and Hairy woodpeckers cannot forage upon. Kisiel (1972) and Williams (1975) have shown that Hairy and Red-bellied woodpeckers choose dead wood for foraging more often than do Downy Woodpeckers on the same study sites.

Our data suggest that relative humidity may influence the distribution of birds in mature deciduous forests during the summer. Although these results concur with other studies that have shown an affect of moisture gradients on bird distribution (Bond 1957, Beals 1960, Smith 1977, Kendeigh and Fawver 1981, Swift et al. 1984), caution should be used when interpreting data gathered over a short time span (see Wiens 1981a).

When avian ecologists consider the distribution and diversity of avian communities, it is not sufficient to study only vegetation characteristics, particularly when researchers are working within similarly structured areas. We agree with the suggestions by Wiens (1981b, 1983), 1) that studying communities on a local scale, rather than on a broad, geographic level, may prove to be more fruitful in delineating factors affecting community organization, and 2) that environmental variations may influence local avian communities within a habitat more than they influence community dynamics on a regional scale.

SUMMARY

The effect of foliage height diversity and atmospheric moisture on avian community structure and composition was studied on 20 0.8-ha plots of mature deciduous forest in northeastern Ohio. Foliage height diversity was not significantly correlated with avian community structure, while relative humidity showed significant positive correlation with species richness. Food resources for leaf-litter foragers and woodpeckers that forage extensively into dead tree trunks and branches may be intimately tied to atmospheric moisture. Such a relationship would indicate that the correlation with species richness is directly with food

supply and only indirectly with relative humidity. Atmospheric moisture may be a useful indicator of avian community composition within geographically and structurally similar deciduous woodlands.

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GENERAL NOTES

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Use of space by territorial male Blue Grouse.—The social system and reproductive behavior of Blue Grouse (*Dendragapus obscurus*) have been studied in several areas of coastal British Columbia (e.g., Bendell and Elliott, Can. Wildl. Serv. Rept. Ser. 4, 1967; Zwickel and Bendell, Proc. XV Int. Ornithol. Congr., The Hague, 15:150–169, 1972; Zwickel et al., pp. 212–225 *in* Symposium on Natural Regulation of Wildlife Populations, F. L. Bunnell, D. S. Eastman, and J. M. Peek, eds., Forest Wildlife and Range Experiment Stn., Univ. Idaho, Boise, Idaho, 1983). The species has a promiscuous mating system (Wiley, Quart. Rev. Biol. 49:201–227, 1974) in which males establish dispersed territories on breeding ranges in spring (Bendell and Elliott 1967; McNicholl, Ph.D. diss., Univ. Alberta, Edmonton, Alberta, 1978). Occupancy of a territory is indicated when males localize their movements within a small area and advertise their presence to females and other males by hooting. These territories function primarily as areas for display and mating, although feeding and other activities also occur in them. Females do not associate with males except to breed. Most hooting is conducted from a few specific locations within the territory (McNicholl 1978); the area encompassing a male's hooting "posts" is his activity center (McNicholl 1978; Lewis and Zwickel, Condor 83:171–176, 1981).

In previous studies the activities of territorial males were followed by observers either working alone or with pointing dogs. These methods have a bias in that birds are more likely to be found when they are hooting than when they are silent. Consequently, they are most likely to be found within activity centers. To overcome this bias I radio-tagged territorial males and was able to address some new questions fundamental to interpretations of the function and importance of territories for male Blue Grouse: (1) where are territorial males located when they are not hooting; (2) are the same areas used consistently throughout the breeding season; (3) what portion of a male's spring/summer home range should be considered a territory? I also examined the activity patterns of males for a relationship between the size of area occupied by individuals and their hooting frequency (e.g., Falls, pp. 61–89 *in* Advances in the Study of Communication and Affect, L. Krames, P. Pliner, and T. Alloway, eds., Vol. 4, Plenum Press, New York, New York, 1975).

Study area and methods.—The study was conducted in 1981 on Hardwicke Island, a 77-km^2 island situated between Vancouver Island and mainland British Columbia (50°27′N, 125°50′W). The study area was ca 56 ha in size and had a vegetation structure and composition similar to that of Jamieson and Zwickel (Auk 100:653–657, 1983).

From 8 to 16 April 1981, 10 adult males were captured with snare poles (Zwickel and Bendell, J. Wildl. Manage. 31:202–204, 1967) and equipped with radio transmitters using a harness attachment (Herzog, J. Wildl. Manage. 43:316–323, 1979). One male was killed by a predator 1 week after being radio-tagged, so on 24 April the transmitter was placed on another bird. Transmitters weighed ca 30 g (less than 2.5% of a bird's weight), and had potential signal ranges of 3 km or more. They were applied only to males that were believed to be territorial; that is, males that were hooting prior to being radio-tagged, or if silent had been identified as adults in a previous year. Most territorial males on my study area were radio-tagged (Fig. 1).

Radio-tagged birds were located with a receiver and hand-held yagi antenna. Their exact locations were determined by taking a compass bearing and pacing to known reference points. I tried to find each male at least once every 3 days. All birds were found about the

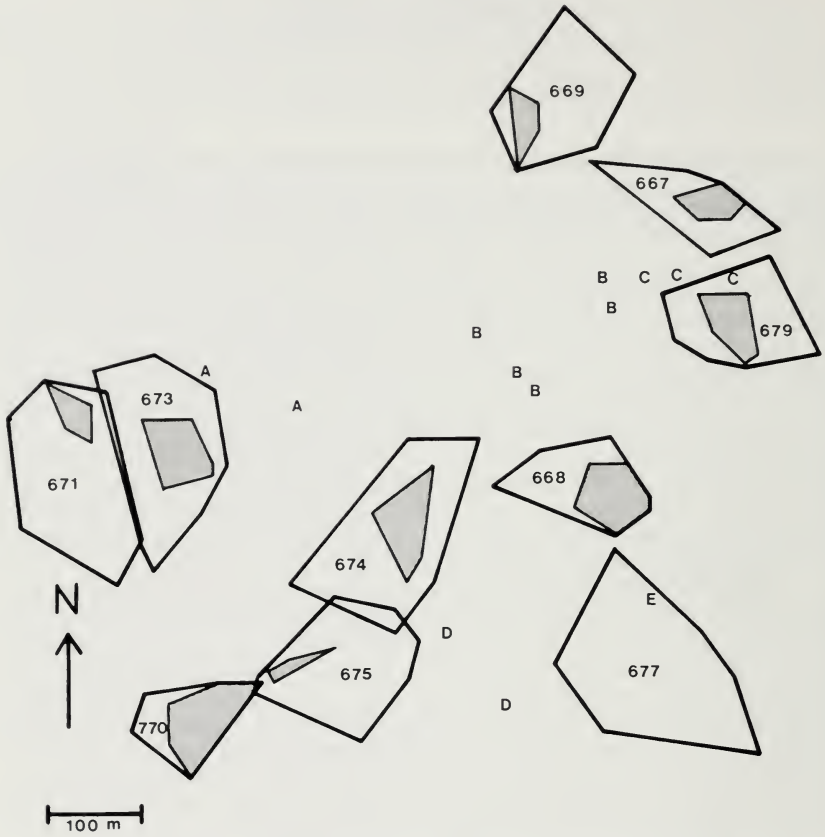

FIG. 1. Spatial relationships of territorial males on Hardwicke Island, British Columbia in 1981. Total home ranges from radio-tagging until territories were abandoned are outlined with solid lines, activity centers are shaded. Numbers identify individual radio-tagged birds and letters represent sightings of non-radio-tagged territorial males.

same number of times except for one with a faulty transmitter (no. 677) and two that were killed by predators (nos. 668 and 770, Table 1). I monitored the whereabouts of surviving birds until late August.

Home ranges were delineated by connecting outermost points of observation with a straight line (Odum and Kuenzler, Auk 72:128–138, 1955; Bendell and Elliott 1967). Sightings that were considered "atypical" (see below) were not used in the analyses. In all instances in which males were observed hooting, they were considered to be doing so within their activity center. Therefore, activity centers were delineated by connecting outermost locations at which males were seen hooting.

In mid-June individual males began leaving their activity centers and immediate vicinities thereof, and moved to new localities. Since they did not subsequently return to their activity centers, I considered them to be abandoning their territories. The length of time between

TABLE 1

SIZE OF HOME RANGES AND DATES OF TERRITORY ABANDONMENT FOR RADIO-TAGGED TERRITORIAL MALE BLUE GROUSE ON HARDWICKE ISLAND, BRITISH COLUMBIA IN 1981

Male	Home range size (ha)			Date of territory abandonment
	Breeding period	Post-breeding period	Radio-tagging to territory abandonment	
667	0.44 (19)[a]	0.29 (21)	0.91 (44)	25 June[c]
668	0.93 (19)	0.36 (9)	[b]	[b]
669	0.58 (19)	0.16 (18)	1.68 (72)	11 August
671	0.26 (16)	1.46 (18)	2.13 (49)	16 July
673	0.73 (21)	1.55 (19)	2.11 (48)	4 July[c]
674	0.64 (16)	2.14 (20)	2.23 (36)	17–18 June[c]
675	0.65 (22)	1.53 (23)	2.00 (63)	20 July
677	0.87 (8)	1.95 (14)	2.75 (25)	25 June[c]
679	0.62 (16)	0.93 (20)	1.31 (40)	27 June
770	0.60 (16)	0.34 (11)	[b]	[b]
Mean	0.63 (17.2)	1.07 (17.3)	1.89 (47.1)	7 July

[a] Number of sightings in parentheses; 24 sightings obtained by observers working with dogs were included when estimating home-range size.
[b] Killed by predator; 668 on 31 May, 770 on 3 June.
[c] Date estimated, ±1–1.5 days.

radio-tagging and abandonment of territories differed among males, so comparisons of home range sizes during this time involve different numbers of sightings per male. I, therefore, examined and compared home range sizes of the 10 radio-tagged males within the periods 8 April–20 May and 21 May–16 June. The first period included the time from radio-tagging of the first male to the end of peak breeding on Hardwicke Island (F. C. Zwickel, unpubl.). Peak breeding is defined as the two week period during which most copulations occur (Zwickel, Condor 79:185–191, 1977). The second time period I examined was from the end of peak breeding to the day before the first male abandoned his territory. Although some copulations took place after 20 May (7.3%), for simplicity I will refer to the periods outlined above as the "breeding" and "post-breeding" periods, respectively.

Results.—All radio-tagged males except one were heard hooting, and some were seen displaying to females or other males. Thus, radio-packages apparently did not preclude the performance of these activities. The individual that was not heard hooting was considered to be territorial because his movements were relatively localized compared to those of non-territorial males (Sopuck, M.Sc. thesis, Univ. Alberta, Edmonton, Alberta, 1979; Jamieson and Zwickel 1983). I may have missed hearing this male hoot as most radio-tracking was done between 09:00 and 17:00 when hooting is less frequent than at other times of the day (McNicholl 1978).

Size of home ranges.—During the breeding period males occupied areas averaging 0.63 ± 0.06 (±1 SE) ha in size (Table 1). Sixty-eight percent (117/172) of the sightings were within activity centers, and activity centers comprised an average of 48.7 ± 9.7% (range = 7.7–100%, male no. 677 excluded) of the area used during this period. Home ranges averaged 1.07 ± 0.24 ha in size during the post-breeding period, an increase of 70% over the breeding period (Table 1); the difference is significant if the two males killed by predators are excluded

TABLE 2

PROPORTION OF SIGHTINGS IN WHICH RADIO-TAGGED TERRITORIAL MALES ON HARDWICKE ISLAND, BRITISH COLUMBIA WERE HOOTING IN 1981

Male	Proportion hooting		
	Breeding period	Post-breeding period	Combined
667	0.63 (16)[a]	0.14 (21)	0.35 (37)
668	0.31 (16)	0.25 (8)	0.28 (25)
669	0.53 (17)	0.17 (18)	0.34 (35)
671	0.39 (13)	0.11 (18)	0.23 (31)
673	0.33 (18)	0.05 (19)	0.19 (37)
674	0.21 (14)	0.15 (20)	0.18 (34)
675	0.14 (21)	0.22 (23)	0.18 (44)
677	0.00 (8)	0.00 (14)	0.00 (22)
679	0.33 (15)	0.10 (20)	0.20 (35)
770	0.67 (12)	0.00 (10)	0.35 (23)
Mean	0.35 (15.0)	0.12 (17.1)	0.23 (32.3)

[a] Number of sightings in parentheses; sightings by observers working with dogs were not included.

(paired t-test, $t = 2.73$, $P = 0.03$). Forty percent (70/173) of the sightings obtained from 21 May–16 June were within activity centers, and 57% (99/173) were in areas used during the breeding period. On average, 76% of the breeding period home range was used again in the post-breeding period. Total home range sizes from 21 May–16 June averaged 1.43 ± 0.21 ha. The increase in size of home ranges after 20 May did not include corresponding enlargements of activity centers. The total area within which males were observed hooting from 8 April–16 June averaged only 7.1% larger than areas used for hooting during the breeding period.

Home range size was not significantly ($P > 0.05$) correlated with the number of sightings per male for either the breeding or post-breeding period. Males were found a similar number of times in both periods (Table 1), so the increase in size of area used after 20 May did not result from the radio-tracking regime.

Up to the time they abandoned their territories, radio-tracked males occupied home ranges that averaged 1.89 ± 0.20 ha (Table 1) in size. Over this time home ranges of radio-tagged males that were adjacent to each other overlapped in only three instances (Fig. 1). Areas of overlap averaged 7.1% of the total area occupied by these males. There was no overlap of activity centers.

Home range size and frequency of hooting.—There was no correlation between the size of a male's breeding or post-breeding period home range (Table 1) and the percent of observations in which he was hooting during these times (Table 2). However, the total area used by radio-tagged males up to 16 June, and up to the time they abandoned their territories, were both inversely related to their frequency of hooting ($r = -0.940$ and -0.803, respectively; both P's ≤ 0.01). For the period 8 April–16 June, size of activity centers was not correlated with percent of observations in which males were hooting.

Abandonment of territories.—The exact date of territorial abandonment was known for four males; others were estimated as midway between the last sighting in the activity center, or its immediate vicinity, and the first sighting in a new locality (times between these dates

ranged from 1 to 3 days). The first and last males to abandon territories did so on 17–18 June and 11 August, respectively (Table 1). Abandonment involved direct moves to new areas, these usually being completed within 2 days of leaving the breeding territory. Three males moved to dense coniferous forest, typical of wintering habitat, whereas the other five moved to new areas on the breeding range. The latter then restricted their movements but did not behave territorially (i.e., were not seen hooting or displaying).

Prior to the time radio-tagged males abandoned their territories, I obtained seven (1.5%, 7/471) "atypical" sightings. Four involved movements in which males crossed activity centers of other males; the other three were instances in which males were found far from their usual areas of occupancy in locations uncharacteristic for territorial males. In all cases, these males were in or near their activity centers when next found. Such sightings may have resulted from males being chased by predators or from chasing conspecifics.

Discussion.—During the breeding period males spent much of their time hooting and most of their movements were restricted to areas within or near activity centers. Hooting diminished in the post-breeding period (Table 2) and there was an increase in home range size. Similarly, males that hooted the most had the smallest home ranges, possibly because their movements were more limited to their activity centers than were those of males that hooted less.

Brown (The Evolution of Behavior, Norton Press, New York, New York, 1975), Wilson (Sociobiology, Harvard Univ. Press, Cambridge, Massachusetts, 1975), and Morse (Behavioral Mechanisms in Ecology, Harvard Univ. Press, Cambridge, Massachusetts, 1980), among others, define territory as an essentially exclusively occupied area that is either actively or passively defended. Other less restrictive definitions also have been proposed (see Kaufmann, Biol. Rev. 58:1–20, 1983 for a review). What portion of a male Blue Grouse's spring/summer home range should be considered a territory: should it consist of the activity center only, or should other areas also be included?

Home ranges of adjacent radio-tagged males overlapped only slightly even when all observations between 8 April and the time territories were abandoned were included. The small degree of overlap that did occur seems inconsequential given that 3 months of sightings were included. Also, males do expel other males from areas outside their activity centers (pers. obs.; see Falls and McNicholl, Can. J. Zool. 57:457–462, 1979). Thus, I suggest that the total area occupied until moving to new areas following the breeding season constitutes a territory.

Nevertheless, the activity center appears to be the focal point of the territory, especially during the breeding period. These centers usually are located on the most elevated portion of the territory, presumably facilitating the broadcasting of hooting and the detection of predators and conspecifics. Their height in relation to surrounding areas is the most critical feature distinguishing territorial sites of high and low quality (Lewis, J. Wildl. Manage. 45: 1048–1051, 1981). Questions that remain, however, and which relate to determining the function of territories, include, why are areas outside of activity centers defended, and why do some males stay on territories longer than others?

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Changes in Five-striped Sparrow song in intra- and intersexual contexts.—Primary song in passerine birds transmits varied information which may have intrasexual and/or intersexual functions, and the types of songs employed have been influenced, in part, by intrasexual and/or intersexual selection. Catchpole (pp. 297–319 *in* Acoustic Communication in Birds, D. E. Kroodsma and E. H. Miller, eds., Academic Press, New York, New York, 1982) discussed the influence of sexual selection on bird song and developed a model which related inter- and intrasexual selection to two main types of song in passerines. In short, intersexual selection involves direct female choice of mate based on males' songs. Primary songs modified for female attraction are long, complex, and variable. Intrasexual selection involves indirect female choice based on the ability of males to repel rival males when obtaining and maintaining control of a territory. Primary songs modified for male repulsion are short, simple, and stereotyped.

Primary songs, however, may have dual functions—one directed at females and one directed at males. In order for this to occur, a bird must be able to change its songs or song patterning accordingly. Birds with single song repertoires can change the character of their delivery only by temporal means or by adding and deleting song components (note complexes). Ficken and Ficken (Behaviour 46:114–127, 1973) demonstrated that Golden-winged Warblers (*Vermivora chrysoptera*), which have simple, stereotyped songs, varied their responses to a playback tape depending on the number of terminal trills included in the playback song. Birds with large song repertoires have more options available to them. In addition to increasing or decreasing the rate of song delivery, the kinds of different song types used can be changed, or the pattern of delivery of the song types can be altered. Marsh Wrens (*Cistothorus palustris*) (Verner, Living Bird 14:263–300, 1975), Eastern Meadowlarks (*Sturnella magna*) (d'Agincourt and Falls, Can. J. Zool. 61:1086–1093, 1982), and Five-striped Sparrows (*Aimophila quinquestriata*; sensu Paynter, pp. 3–214 *in* Checklist of Birds of the World, R. A. Paynter, Jr. and R. W. Storer, eds., Harvard Univ. Press, Cambridge, Massachusetts, 1970) (Groschupf and Mills, Condor 84:226–236, 1982) vary their song bouts in this manner.

Yet another way of producing differences in songs and song bouts is to change the ordering of within-song components. This rarely occurs, as most birds have highly ordered note complexes within songs, but it does occur in at least two species, the Sedge Warbler (*Acrocephalus schoenobaenus*) (Catchpole, Behaviour 59:226–245, 1975) and the Five-striped Sparrow (Groschupf and Mills 1982). Five-striped Sparrow songs consist of an introductory note followed by one–six (usually two) note complexes. An individual has approximately 200 different song types which are comprised of about 45 different note complexes. New songs are made up of reordered note complexes rather than new note complexes. Song bouts may consist of one song type sung repeatedly or they may consist of several different song types sung in an unpredictable pattern. The purpose of this study was to determine whether Five-striped Sparrow note complex and song type use and delivery within songs and bouts were related to intra- or intersexual contexts. Using Catchpole's (1982) model, one would predict that songs and song bouts sung in an intrasexual context (those sung in response to playback of male's song) would be less variable and more simple than those sung in an intersexual context (those sung in the presence of a female).

Methods.—A "population" of Five-striped Sparrows southwest of Patagonia, Santa Cruz Co., Arizona, provided an ideal situation for the study. The "population" consisted of one pair of birds; the nearest known Five-striped Sparrows were located at Chino Canyon, 24 km NW of Patagonia (Mills, Western Birds 8:121–130, 1977). Thus, there were no male/male interactions possible during the study period. The male, SC8, was recorded 10 May–

28 July 1978. Most recordings were of spontaneous songs, but on a few occasions playback songs were used, and they now provide the basis for intrasexual interactions in this study.

Song bouts used for data analyses were selected based on the following requirements: (1) song bouts consisted of at least 10 songs; (2) both pre- and post-playback songs were recorded; (3) pre-playback songs were sung spontaneously and in the presence of SC8's mate; and (4) playback consisted of SC8's pre-playback song bout. Only five situations on four different dates were found which met all these requirements. Since members of a pair are rarely separated (Mills et al., Living Bird 18:95–110, 1980), in all situations SC8 was either singing while foraging with his mate, or he was singing perched near the foraging female. Playback was performed while SC8 was in view, and it was played inside his territory boundary. Five-striped Sparrows do share some note complexes. Of 81 different note complexes sung by three different males, 15 note complexes were shared by all three males (Groschupf and Mills 1982). Therefore, by using SC8's recently sung songs as playback, the possible effect that "unrecognizable" note complexes (those not included in SC8's repertoire) might have on his response would be eliminated. A maximum of 20 songs from each bout (those either immediately preceding or immediately following playback) was used. Song bouts sung during pre- and post-playback were sonagraphically analyzed to determine the types and numbers of songs and note complexes used. Songs were recorded with a 110 Sony cassette tape recorder at a tape speed of 18.7 cps with a Gibson EPM microphone and were analyzed with a Kay Elemetrics Company model 6061A Sona-Graph at the wide band-pass setting and by listening to playbacks at one quarter (4.5 cps) speed.

Results.—Song playback induced an immediate change in SC8's behavior. Upon hearing playback, he flew or sneaked silently along the ground towards the speaker, and then began to vocalize as he approached to within 10 m. Initial vocalizations included *chucks, pips,* "alarm," and "pair bond" calls (Groschupf and Mills 1982) which were sometimes interspersed later between songs. It was shown previously for Five-striped Sparrows that there is a negative relationship between song pattern variability and intersong interval (Groschupf and Mills, Auk 95:758–760, 1978), but a comparison of intersong intervals or singing rates of songs sung before and after playback would not be valid in the present study because of the inclusion of non-song vocalizations (e.g., *chucks,* "alarm" calls). Delivery of songs within bouts which do not include other vocalizations may be faster, or even slower, than song bouts which do.

The data show that all songs and song bouts sung immediately after playback were less variable and more simple than those sung preceding playback, as predicted. The numbers of different song and note complex types used after playback were significantly less than the numbers used prior to playback (for each, $P < 0.05$, one-tailed Wilcoxon paired sample test [Zar, Biostatistical Analysis, Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 1974]) (Table 1). Pre-playback songs consisted of one–five note complexes; post-playback songs consisted of only one–three note complexes. Of the total songs recorded, post-playback songs almost always (90%) were comprised of only one note complex type, whereas prior to playback, songs often (43%) consisted of more than one note complex type which were sung in various positions within songs in a given bout (Table 2). Because almost all post-playback bouts consisted of songs comprised of only one or two note complexes (95%), as compared to the pre-playback bouts which consisted of several three, four, and five note complex songs (37%), post-playback songs tended to be shorter than pre-playback songs. In addition, SC8 often sang different note complexes, and hence, songs, during playback than during pre-playback even though the songs he had heard during playback were the same as those he had just sung (Table 2).

Discussion.—Five-striped Sparrow songs and song bouts are variable in the type, number, and sequence of note complexes used. Complexity and versatility of song bouts, as measured

TABLE 1

QUANTITATIVE SUMMARY OF SONG AND SONG BOUT CHARACTERISTICS BEFORE (PR) AND AFTER (PO) PLAYBACK

	10 May		10 May		21 May		19 July		28 July		Total	
	Pr	Po	Pr	Po	Pr	Po	Pr	Po	Pr	Po	Pr	Po
No. of songs in bout	13	20	20	20	12	10	16	18	20	12	81	80
No. of diff. songs	5	2	6	2	4	4	8	3	11	6	30	10
No. of diff. note complexes	3	2	4	1	5	4	4	3	3	2	16	7
% of total songs with 1 note complex	23	100	55	10	17	10	6	6	0	17	21	33
% of total songs with 2 note complexes	77	0	45	90	83	90	13	94	15	50	42	63
% of total songs with 3 note complexes	0	0	0	0	0	0	69	0	55	33	27	5
% of total songs with 4 note complexes	0	0	0	0	0	0	13	0	25	0	9	0
% of total songs with 5 note complexes	0	0	0	0	0	0	0	0	5	0	1	0
% of total songs with 1 note complex type only[a]	100	100	100	100	58	50	75	100	45	100	90	57

[a] This category consists of single or multiple note complex songs, e.g., L, LL, LLL, J, JJ, JJJ, etc.

by total versatility, were previously shown to be related to nesting stages (Groschupf and Mills 1982). Total versatility values, which are the product of song type versatility and transition versatility (Kroodsma and Verner, Auk 95:703–716, 1978), were significantly higher when eggs or young were in the nest than when no nest or just a nest was present. It was proposed that the complexity of the song bouts stimulated females to begin incubation, to further egg-lay, or to maintain the pair bond. Thus, the increased complexity and versatility of singing performances had an intersexual function.

Intersexual function of large song repertoires has been shown in at least two bird species. It was experimentally demonstrated that Sedge Warblers (Catchpole, Behaviour 74:149–166, 1980) and Northern Mockingbirds (*Mimus polyglottos*) (Howard, Evolution 28:428–438, 1974) with large song repertoires obtained mates sooner than males with small repertoires.

Large song repertoires also have been shown to have intrasexual functions. It was shown experimentally that areas occupied by loudspeakers emitting Great Tit (*Parus major*) recordings consisting of many song types were settled last by newly arriving male Great Tits, whereas those areas broadcasting single song type repertoires were settled first (Krebs, pp. 47–62 *in* Evolutionary Ecology, B. Stonehouse and C. Perrins, eds., Macmillan, New York, New York, 1977). The effect of large song repertoires repelling rival males also has been shown experimentally in Red-winged Blackbirds (*Agelaius phoeniceus*) (Yasukawa, Anim. Behav. 29:114–125, 1981).

TABLE 2

SONG TYPES USED IN EACH SONG BOUT BEFORE (PR) AND AFTER (PO) PLAYBACK

10 May		10 May		21 May		19 July		28 July	
Pr	Po	Pr	Po	Pr	Po	Pr	Po	Pr	Po
A[a] (1)[b]		C (2)		GG (4)	GG (1)	NNN (2)		LL (2)	LL (3)
AA (5)		D (4)		HI (5)	HI (5)	ONNN (2)		LLJ (3)	
BB (5)		DD (6)		JJ (1)	JJ (3)	O (1)		LLJJ (2)	
C (1)	C (19)	E (2)		K (2)		OO (1)		LLMM (1)	
B (1)		EE (3)			J (1)	OJJ (1)		LJJ (1)	
	L (1)	F (3)				JJ (1)	JJ (8)	JJJ (5)	JJJ (3)
			L (1)			JJJ (7)		JJL (1)	
			LL (19)			JJP (1)		JLL (1)	
							BB (9)	JJJL (2)	
							C (1)	JJLL (1)	
								JJJLL (1)	
									L (1)
									LLL (1)
									J (1)
									JJ (3)

[a] Different letters represent different note complex types. A song consists of 1–5 note complexes.
[b] Number in parentheses is the number of times the song was used in the song bout.

In each of the preceding examples, the primary song of each species was demonstrated to have either an intrasexual or an intersexual function; none showed that primary songs serve a dual function. Dual function of primary song has been experimentally demonstrated in the Cuban Grassquit (*Tiaris canora*). Songs used to court females are longer and contain more syllable types than those which are used in male/male interactions (Baptista, J. Ornithol. 119:91–101, 1978). In the present study, it was shown that a Five-striped Sparrow changed the complexity of his songs and song bouts according to the context in which they were sung. The songs of males singing in the presence of a female, consisted of numerous note complex types occurring together within a song, and song bouts consisted of many nonrepetitive song types. During a male/male interaction (i.e., after playback), the songs and song bouts became less complex and more stereotyped. Songs often consisted of only one note complex type and, within a song bout, song types were sung repetitively. Thus, it appears that songs of Five-striped Sparrows play a dual role and are influenced by both intra- and intersexual selection; their songs are short, simple, and stereotyped when used for male repulsion, and are longer, more complex, and variable when used for female attraction or stimulation. This may be the first evidence of a species exhibiting repertoire elasticity within songs, as well as between bouts, and how it is related to the sexual context in which it occurs.

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Sandhill Crane use of nest markers as cues for predation.—Many authors have raised concerns about increased nest predation on study species as a result of investigator activities. Examples include research on waterfowl (e.g., Hammond and Forward, J. Wildl. Manage. 20:243–247, 1956; Strang, J. Wildl. Manage. 44:220–222, 1980), larids (e.g., Robert and Ralph, Condor 77:495–499, 1975; Fetterolf, Wilson Bull. 95:23–41, 1983), and passerines (e.g., Lenington, Auk 96:190–192, 1979), but see Nichols et al. (Auk 101:398–402, 1984). Although increased nest predation has often been observed, there is little information about how the predators are attracted to nests. I describe here direct observations of a Sandhill Crane (*Grus canadensis*) locating shorebird nests by cueing in on nest markers.

The observations were made in 1983, during a study of breeding Red-necked Phalaropes (*Phalaropus lobatus*) at the Queen's University Tundra Biology Station at La Pérouse Bay, 40 km east of Churchill, Manitoba (58°24′N, 94°24′W). The 2-km^2 study area is in the delta of the Mast River, characterized by numerous small islands dominated by 0.2–1.0 m high willow (*Salix brachycarpa*) and dwarf birch (*Betula glandulosa*), and sedges (e.g., *Carex aquatilis*). A more detailed description of the study area is provided by Jefferies et al. (Can. J. Bot. 57:1439–1450, 1979).

From mid-June to late July, the locations of 50 phalarope nests and 130 Semipalmated Sandpiper (*Calidris pusilla*) nests were marked with 50-cm high unpainted wooden stakes that were placed 2–3 m south to southeast of each nest. In addition, 3061 Snow Goose (*Chen caerulescens*) nests were staked similarly on the shorebird site and in the surrounding

area. There were 150–200 other stakes in the area, marking nest sites used by geese and shorebirds in previous years, as well as banding locations for Willow Ptarmigan (*Lagopus lagopus*).

On 13 July at 18:45 EST, I observed two Sandhill Cranes walking through the study area. Detailed observations were made on the individual nearest to me for 45 min, during which it walked approximately 600 m. The crane usually moved slowly with its head bent close to the ground, occasionally probing vegetation. Its searching pattern was occasionally punctuated by greatly intensified searches which consisted of the bird moving back and forth quickly over areas approximately 2 m^2, peering at the ground intently for 30–60 sec at a time. These intensive searches occurred at only seven specific locations; all were around nest stakes. All nest stakes within 25 m of the crane were explored by the bird. Four of the seven stakes marked Semipalmated Sandpiper nests, in three of which the eggs had hatched previously; the eggs in the fourth had already been taken by an unknown predator. Two of the seven markers indicated phalarope nests, both of which contained eggs. The seventh stake had been used the previous year to mark a Snow Goose nest. On two occasions the crane ran very quickly toward nest stakes from 15 to 20 m away, immediately adopting its intensified search behavior upon reaching the stake.

No predations were observed directly. Although my view of the crane was obscured by vegetation when it investigated the first nest, I later discovered that the eggs from this phalarope nest had, in fact, been taken. The other active nest was well concealed and apparently overlooked by the crane. However, an immediate inspection of the other phalarope nests that had been active when checked within the previous 2 days revealed that the contents of 7 of 19 nests had been preyed upon. The ground around three of these depredated nests was perforated by holes like those made by a crane probing with its bill. The eggs in most Semipalmated Sandpiper nests had already hatched prior to this observation (C. L. Gratto, pers. comm.).

All shorebird nest markers were removed immediately, and in the ensuing weeks the contents of only one more nest were preyed upon; the eggs in the other 11 hatched, as did eggs in three more nests discovered after 13 July. This drop in predation may not have been due to the absence of markers, but of the cranes themselves, since they were not seen again on the study area after I flushed them following my initial observations.

These observations extend previous reports concerning the opportunistic nature of Sandhill Crane feeding behavior. In addition to eating a large variety of plants and invertebrates (Walkinshaw, The Sandhill Crane, Cranbrook Inst. Sci. Bull. 29, 1949; Mullins and Bizeau, Auk 95:175–178, 1978), Sandhill Cranes have preyed upon ducklings (Littlefield, Wilson Bull. 88:503–504, 1976), Canada Goose (*Branta canadensis*) eggs (Hoffman, Wilson Bull. 92:122, 1980), Willow Ptarmigan chicks, and Snow Goose eggs (Harvey et al., Wilson Bull. 80:421–425, 1968).

My observations also provide evidence that Sandhill Cranes are capable of associating a food source with a particular (in this case artificial) visual cue. This is analogous to experimental findings on associative learning in Carrion Crows (*Corvus corone*) (Croze, Searching Image in Carrion Crows, Paul Parey, Berlin, 1970). An interpretation of associative learning, rather than simply a strategy of investigating novel stimuli regardless of past experience, is suggested because the crane ignored other novel items such as brightly colored flagging tape and 1-m high blue stakes marking locations where adult ptarmigan were captured. Although cranes had been seen regularly in the surrounding area before these observations, they were seen only briefly twice on the shorebird study area 5 and 8 days before. Prior to this observation, cranes may have associated markers with Snow Goose nests outside the study area, although such depredations had never been observed. However, in 1984 two cranes were seen taking Snow Goose eggs on one occasion (R. F. Rockwell, pers. comm.). On the

day the phalarope nests were preyed upon, no Snow Goose nests were active, and only approximately 7% of all markers in the shorebird study area indicated nests containing eggs.

Three explanations other than nest markers being used to detect the nests may be discounted: (1) habitat cues were unlikely because of the varied nature of nest sites ranging from damp sedge areas to drier sites dominated by willows; (2) trails in the vegetation, resulting from our visits, were minimized because all nests were on small islands, and many were checked by us without walking on land; (3) even if Sandhill Cranes possess a sufficiently developed olfactory system, in most cases scents were not available since terminated nests had not been visited for weeks, and the abandoned Snow Goose nest was ignored by us all season.

Nest markers have seldom been shown conclusively to be of importance as cues to predators in nest predation, although it has frequently been acknowledged that markers pose a potential problem, particularly for such opportunistic predators as corvids (Hammond and Forward 1956). Picozzi (J. Wildl. Manage. 39:151–155, 1975) used artificial nests resembling those of Red Grouse (*Lagopus l. scoticus*) to study predation on marked and unmarked nests and found Carrion Crows learned to locate nests by the presence of brightly marked nest stakes. Predation was higher in marked than unmarked nests, even when markers were placed 10 and 20 m away. A similar study of predation on Sage Grouse (*Centrocercus urophasianus*) nests by Common Ravens (*Corvus corax*) suggested similar conclusions (Autenrieth, Sage Grouse Management in Idaho, Idaho Dept. Fish and Game, Wildl. Bull. No. 9, 1981).

Generally, birds which use active defense or inaccessibility to deter predation (e.g., most colonial species) will not be affected as strongly by nest markers. However, the evidence presented here of opportunistic predation by cranes, and the findings of others on corvids suggests that investigators studying birds that rely primarily upon crypsis for nest defense should be particularly cautious with nest markers.

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Northern Harrier kills Sandhill Crane.—On 2 August 1983 I observed an adult female Northern Harrier (*Circus cyaneus*) attack and kill a 5-week old Sandhill Crane (*Grus canadensis*). This attack occurred at approximately 10:00 at the Big Hole National Battlefield, 19 km west of Wisdom, Beaverhead Co., Montana. The juvenile crane was accompanied by two adults and one other juvenile. The cranes were foraging in a wet meadow at the time of the attack.

The young cranes were approximately 8 m from the adults and 2 m apart when the harrier made four passes to within 1 m and attacked. Both juvenile cranes looked up at the harrier as it passed overhead; the crane that was being attacked crouched down during the passes, while the other juvenile watched passively. The adults continued feeding, seemingly unaware

of the harrier's presence. On the fifth pass the harrier seized the young crane and held it on the ground for 5–6 sec. An adult crane approached within 3 m and the harrier flew off without the victim. Neither of the adults displayed any of the typical defensive postures described for cranes by Layne (Fla. Field Nat. 9:51–75, 1981). Both adults called periodically and all three cranes stayed near the victim until 12:00 when I approached the site. The attacked crane was dead, with several deep punctures at the base of the neck. The dead bird measured 67.5 cm from bill tip to base of feet and, based on size, was estimated to be 5 weeks old.

Food habits of the Northern Harrier are well documented (Errington and Breckenridge, Amer. Midl. Natur. 17:831–848, 1936; Bent, U.S. Natl. Mus. Bull. 167, 1937; Randall, Wilson Bull. 52:165–172, 1940; Schipper et al., Ardea 63:1–29, 1975). Accounts of avian predation on Sandhill Cranes have not been documented, although a recent study has identified the Great Horned Owl (*Bubo virginianus*) as a source of crane chick mortality (C. D. Littlefield, pers. comm.).

Judging from the adult cranes' behavior prior to the attack, the Northern Harrier may not be regarded as a predator. However, this observation may represent atypical parental behavior, and the paucity of records of such events recorded may be due to the difficulty of observing cranes in the tall vegetation that characterizes their nesting habitat. Hence, harrier attacks, such as the one reported here, may be more frequent than the literature suggests.—David L. Genter, *Dept. Zoology, Univ. Montana, Missoula, Montana 59812.* *Accepted 26 Nov. 1984.*

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Water-crossing behavior of raptors during migration.—Migration pathways of many birds are known to be influenced by large bodies of water (Ralph, Bird-Banding 49:237–247, 1978). The best example of lakes and oceans acting as barriers to migration is the aggregations of Falconiformes along coastlines and at the end of peninsulas (Allen and Peterson, Auk 53:393–404, 1936; Haugh and Cade, Wilson Bull. 78:88–110, 1966; Evans and Lathbury, Ibis 115:572–585, 1973; and summarized by Newton, Population Ecology of Raptors, Buteo Books, Vermillion, South Dakota, 1979). While some species are reluctant to cross water, others make long distance flights (>100 km) over water (Williamson, Br. Birds 47:434–441, 1954; Brown and Amadon, Eagles, Hawks and Falcons of the World, McGraw-Hill, New York, New York, 1968; Moreau, The Palearctic-African Bird Migration Systems, Academic Press, New York, New York, 1972; Beamon and Galea, Ibis 116:419–431, 1974; Walter, Eleonora's Falcon, Univ. Chicago Press, Chicago, Illinois, 1979; Kerlinger et al., Auk 100: 488–490, 1983). Few studies have been conducted to determine what species undertake water crossings and under what conditions birds cross (Kerlinger, Anim. Behav. 32:1029–1034, 1984). In this paper I report on the water crossing tendencies of 10 Falconiform species during migration at two locations in North America. In addition, I test the hypothesis that long, narrow-winged species undertake water crossings more readily than species with low aspect ratio.

Methods.—Study sites were located at Whitefish Point, Chippewa Co., Michigan (46°40′N, 84°57′W) for spring migration (27 April–6 May 1981) and at Cape May Point, Cape May Co., New Jersey (38°56′N, 74°58′W) for autumn migration (3 September–13 October 1980). Upon reaching the ends of these peninsulas, migrants must either cross >18 km of water or fly hundreds of km around Lake Superior or Delaware Bay in directions that are inappropriate for migration. The crossings are similar in distance (18.2 km at Cape May and

17.7–26.7 km at Whitefish depending upon flight direction) and the destinations are visible except during periods of rain, fog, or haze. At Cape May strong NW–W winds could potentially blow a migrant out over the Atlantic Ocean, while E–SE winds might push birds over Delaware Bay. With strong SE–E winds at Whitefish, birds could be blown out over the main body of Lake Superior. For a more complete description of the crossings see Kerlinger (1984).

Observations were conducted from 07:00–16:00 EST. Migrant raptors were observed with the naked eye as they approached the end of the peninsulas and with 7× binoculars as they moved offshore. When birds approached within approximately 200 m of the shoreline (marked by houses at Cape May and a treeline at Whitefish) they were considered subjects for the study. Once a migrant or flock of migrants passed this line their behavior was observed and recorded. As birds left the shoreline I made a visual assessment of flight altitude as follows: <5 m above the water, 5–30 m, 30–100 m, >100 m yet easy to see without binoculars, and difficult to see without binoculars.

To test the hypothesis that the tendency of a species to make water crossings is related to the species' flight morphology I regressed aspect ratio (of each species) on the proportion (arcsine transformed) of each species that crossed Delaware Bay and Lake Superior. The rationale for using aspect ratio (span^2/wing area) is that it is a relative measure of wing length and width. Birds such as gulls (Larinae), terns (Sterninae), and tubenoses (Procellariiformes), that spend a large proportion of their lives flying over water, are usually long winged with high aspect ratios, while landbirds generally tend to have shorter wings of lower aspect ratio (Savile, Evolution 11:212–224, 1957; Warham, New Zealand J. Zool. 4:78–83, 1977). Thus, a positive relationship (regression coefficient) is predicted if longer winged species cross water more often than shorter winged species. Wing spans were obtained from labels on specimens in the Vertebrate Museum of the University of California at Berkeley, and from recently acquired specimens that I obtained in New York and South Carolina. Wing areas were from Poole (Auk 55:511–517, 1938) and from fresh specimens from New York and South Carolina. Because male and female raptors differ in size, I computed the mean span and wing area of all male and female specimens of each species ([mean of males + mean of females]/2) to compute aspect ratio.

Results and discussion.—All species made water crossings on some occasions (Table 1). The tendency to cross Lake Superior or Delaware Bay varied greatly among species with some crossing infrequently (Turkey Vultures, Red-tailed and Broad-winged hawks), others crossing more often (Merlins, American Kestrels, Sharp-shinned and Rough-legged hawks), and others that usually made crossings (Peregrine Falcons, Northern Harriers, Ospreys). The tendency of a given species to cross was a positive function of aspect ratio (Fig. 1), a result that is consistent with the hypothesis that birds with relatively long wings (similar to seabird morphology) are more likely to cross water barriers than species with relatively short wings.

When encountering the shoreline, Northern Harriers, Peregrine Falcons, Ospreys, and Merlins rarely hesitated to fly out over water, while Turkey Vultures, American Kestrels, Broad-winged and Sharp-shinned hawks usually hesitated before venturing out over water, or turning back inland. An attempt was made to quantify the behavior of migrants at the shoreline, but behavior was so variable that this was not possible. Behavior included soaring in one place over the ground, flight back and forth along the shore, gaining altitude while flapping into the wind, soaring to great altitudes, descending to eye level, perching on driftwood or other objects, and hunting along the treeline or dunes. Hunting near the shoreline was obvious among Northern Harriers, Merlins, American Kestrels, and Sharp-shinned Hawks.

When individual migrants did fly out over water some returned after flying varying distances from shore. Some individuals, especially Broad-winged Hawks and Turkey Vul-

TABLE 1
SUMMARY OF WATER CROSSING BEHAVIOR OF MIGRATING HAWKS AT CAPE MAY AND WHITEFISH POINTS

Species	N	% cross	% not leave shore	% out over water and back
Turkey Vulture (*Cathartes aura*)	31	10	64	26
Osprey (*Pandion haliaetus*)	83	93	5	2
Northern Harrier (*Circus cyaneus*)	112	93	4	3
Sharp-shinned Hawk (*Accipiter striatus*)	7648	71	17	12
Broad-winged Hawk (*Buteo platypterus*)	2123	26	33	41
Red-tailed Hawk (*B. jamaicensis*)	55	11	47	42
Rough-legged Hawk (*B. lagopus*)	125	69	17	14
American Kestrel (*Falco sparverius*)	764	66	25	9
Merlin (*F. columbarius*)	46	76	15	9
Peregrine Falcon (*F. peregrinus*)	14	100	0	0

tures, disappeared toward the opposite shore before returning (Table 1). Flocks of these two species returned to shore approximately 10 min after leaving on at least three occasions.

Regardless of whether the migrant returned or crossed, all species employed continuous flapping or intermittent flap-and-glide flight over water. When leaving the shore, Turkey Vultures usually employed gliding flight, but when returning to shore their flight incorporated intermittent bouts of flapping. A most unusual mode of flight was employed by at least three Peregrine Falcons as they disappeared out over the Atlantic Ocean at Cape May. The downwind soaring flight of Peregrine Falcons was very different from soaring flight over land in that the circles (more accurately called trochoids) were along a vertical axis of 20–40° to the water that took them to within 2 m of the waves at the lowest point and about 10 m at the highest. Some flapping was noted during that phase of the circle that altitude was gained, at which time birds faced into the wind. This mode of soaring was suggestive of dynamic soaring (Pennycuick, pp. 1–73 *in* Avian Biology, Vol. 5, D. S. Farner and J. R. King, eds., Academic Press, New York, New York, 1975) with some powered flight involved. It is also possible that lift was gained by static soaring in updrafts created by wind deflected off the waves. Both static and dynamic soaring are less energetically expensive than powered flight, but dynamic soaring would only be possible when the wind was blowing toward the appropriate direction for migration. No other species were seen soaring when over water, except Ospreys that appeared to be foraging, so it is not likely that many raptors found thermals over the water.

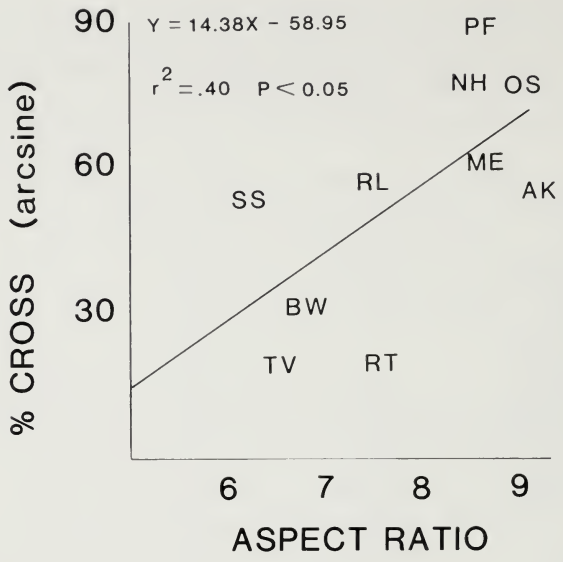

FIG. 1. Relationship between the percentage of each species that made crossings and that species' aspect ratio. (PF = Peregrine Falcon, NH = Northern Harrier, OS = Osprey, ME = Merlin, RL = Rough-legged Hawk, AK = American Kestrel, SS = Sharp-shinned Hawk, BW = Broad-winged Hawk, RT = Red-tailed Hawk, TV = Turkey Vulture.)

Because so little soaring occurred over water, the altitude of flight at the initiation of crossings was the same as over land or lower and varied considerably. No Turkey Vultures, Rough-legged, Red-tailed or Broad-winged hawks flew within 5 m of the waves, but varying percentages of the other species did so: Peregine Falcon, 23%; Osprey, 9%; Northern Harrier, 22%; Merlin, 34%; Sharp-shinned Hawk, 5%; American Kestrel, 19%. The positive correlation between the proportion of each species that crossed and the proportion seen below 5 m (both arcsine transformed) was significant ($r = 0.74$, N = 10, $P < 0.01$), an indication that those species that crossed most often were more likely to fly at very low altitudes. Flight at <5 m above the water made raptors difficult to detect at times. Flight at high altitudes also made raptors difficult to detect and undoubtedly biased observations to lower flying birds. On a few occasions Broad-winged Hawks (including one flock of >500) at Whitefish and Sharp-shinned Hawks (once >300 within 1 h) at Cape May were noted initiating crossings at such heights that they were nearly undetectable with the unaided eye, even when directly overhead. Kerlinger (1984) noted that a significantly larger proportion of Sharp-shinned Hawks tended to cross Lake Superior and Delaware Bay when they approached the shoreline at high altitudes as opposed to low altitudes. Thus, it is possible that a much larger number of birds crossed Lake Superior and Delaware Bay than was estimated in this study.

In addition to variability in altitude of flight, there were at least four other factors that potentially influenced the accuracy of assessing the numbers and proportions of raptor species that made crossings at Whitefish and Cape May Point: (1) Birds flying inland after encountering Lake Superior or Delaware Bay may have been counted several times before crossing (Kerlinger and Gauthreaux, Anim. Behav. 32:1021–1028, 1984). (2) Individuals of species

that forage over water may have been counted incorrectly as migrants returning to shore. I witnessed successful hunting forays by a Peregrine Falcon (capturing a warbler-sized bird) and an American Kestrel (carrying a Tree Swallow [*Tachycineta bicolor*]) over water, as well as several unsuccessful attempts at avian prey by Merlins. (3) Birds migrating in rain or fog were more difficult to detect than when visibility was better. Of the seven Merlins and one Peregrine Falcon I saw flying over water during steady rainfall, all were difficult to observe and some would not have been detected at distances >300 m. (4) Finally, individuals of some species (particularly Peregrine Falcons) may have initiated crossings at Whitefish and Cape May before arriving at the ends of the peninsulas and were never observed (P. Dunne, pers. comm.).

The results of the present study strongly suggest that the tendency of a species to undertake water crossings is related to its morphology. Longer-winged species, often with pointed wings, have high aspect ratios that decrease induced drag and therefore the energetic cost of powered flight (Pennycuick 1975). Reduced cost of flight and low drag coefficients may permit long-winged species to soar in weak updrafts, and thus promote longer distance flight over water. The finding that falcons and Ospreys regularly undertake water crossings is in agreement with findings by Kerlinger et al. (1983), although the Northern Harrier was conspicuously absent from their species list from the North Atlantic Ocean. A list of raptor migrants from the island of Malta also shows that the long, narrow-winged falcons, Ospreys and kites are more likely to cross the Mediterranean Sea than are the wider-winged buteos, accipiters, eagles, and vultures (Beaman and Galea 1974). Whether this relationship is a general one can only be determined by tests at crossings of varying distances in which many species are examined. Future studies should test this relationship and investigate why water crossings are effective barriers to migration and dispersal.

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Sex ratios in broods of Cooper's Hawks.—Adult female Cooper's Hawks (*Accipiter cooperii*) are about 1.5 times as heavy as males (Brown and Amadon, Eagles, Hawks and Falcons of the World, McGraw-Hill, New York, New York, 1968) and in the nest the females are noticeably larger at one week of age. Meng (Ph.D. diss., Cornell Univ., Ithaca, New York, 1951) reported a virtually even sex ratio (35 males, 36 females) in 20 broods of Cooper's Hawks in New York, but he did not determine if this ratio resulted from differential mortality at either the egg or nestling stage. Lack (The Natural Regulation of Animal Numbers, Oxford Univ. Press, London, England, 1954) suggested that male raptors might have lower survival rates in the nest because larger females would be more successful in competition for food. If so, the sex ratio at conception might be biased toward males (Newton, Population Ecology of Raptors, Buteo Books, Vermillion, South Dakota, 1979). Newton and Marquiss (Am. Nat. 113:309–315, 1979) failed to find such a bias in eggs of European Sparrowhawks

TABLE 1

SEX RATIO IN BROODS OF COOPER'S HAWKS IN DIFFERENT YEARS IN WISCONSIN[a]

Year	No. of broods	Total males	Total females	Males : females
1980	9	14	15	0.9:1.0
1981	16	42	24	1.8:1.0
1982	20	30	37	0.8:1.0
1983	26	51	43	1.2:1.0
Total	71	137 (53.5%)	119 (46.5%)	1.2:1.0

[a] There was no significant difference in the sex ratio among years ($\chi^2 = 5.20$, df = 3, $P \geq 0.05$), nor did the 4-year ratio differ significantly from a hypothesized 1:1 ratio ($\chi^2 = 1.27$, df = 1, $P \geq 0.05$).

(*Accipiter nisus*). Here, we present data on the sex ratios of 71 broods of Cooper's Hawks observed in Wisconsin during 1980–1983.

Sexing was done at the time of banding, when the young were at least two weeks old. We determined the sex ratio in eggs from 24 of the 71 nests in which clutch size was known, all eggs hatched, and all young survived to banding age (cf. Newton and Marquiss 1979). At 13 of the 71 nests, clutch size was known but mortality occurred at the egg or early nestling stages; clutch size was not known at the remaining 34 nests.

The number of nestlings examined included 137 (53.5%) males and 119 (46.5%) females. We found no significant difference in sex ratios among years (Table 1). Therefore we pooled our data for the remaining analyses. The overall 1.2:1.0 male/female ratio is not significantly different from unity (Table 1).

Broods ranged from one to six nestlings. We suspect that many of the smaller broods resulted when larger clutches suffered losses during the egg or nestling stage, as nests with clutch sizes of four and especially five eggs were common in our study (unpubl. data). The sex ratio of small broods did not significantly differ from that of larger broods (Table 2). We found no marked surplus of either sex at laying and no significant difference between this sex ratio and that in broods with known egg or nestling mortality (Table 3). We conclude that there was no differential mortality between the sexes up to the time of banding.

TABLE 2

SEX RATIO IN DIFFERENT BROOD SIZES OF COOPER'S HAWKS IN WISCONSIN[a]

Brood size	No. of broods	Total males	Total females	Males : females
1	1	1	0	
2	12	12	12	1.0:1.0
3	18	30	24	1.3:1.0
4	24	49	47	1.0:1.0
5	15	41	34	1.2:1.0
6	1	4	2	2.0:1.0

[a] There was no significant difference in the sex ratio among broods of different sizes ($\chi^2 = 0.47$, df = 3, $P \geq 0.05$); brood sizes of 1 and 6 young were excluded from analysis because of small sample sizes.

TABLE 3

SEX RATIO IN BROODS WITH NO MORTALITY UP TO BANDING COMPARED TO THAT IN BROODS WITH MORTALITY AT DIFFERENT STAGES[a]

Brood category	No. of broods	Total males	Total females	Males : females
No mortality at egg or early nestling stage[b]	24	54	52	1.0:1.0
Mortality only at egg stage	8	15	10	1.5:1.0
Mortality only at nestling stage	5	5	6	0.8:1.0
Total	37	74 (52.1%)	68 (47.9%)	1.1:1.0

[a] There was no significant difference in the sex ratio among the different categories ($\chi^2 = 0.85$, df = 2, $P \geq 0.05$), nor from a hypothesized 1:1 ratio ($\chi^2 = 0.26$, df = 1, $P \geq 0.05$).
[b] Equals sex ratio in the egg.

There probably was some mortality of young during the time between banding and fledging. Snyder and Wiley (Ornithol. Monogr. 20, 1976) reported a high mortality during the late nestling stages for Cooper's Hawks in Arizona and New Mexico, and they observed cannibalism within broods, apparently as a result of food stress. They did not, however, indicate the sex of surviving nestlings and there is no evidence that nearly fledged male Cooper's Hawks have a higher mortality rate than females. Furthermore, Meng (1951) reported that in recently fledged Cooper's Hawks, the most aggressive (and probably the "hungriest") youngster, irrespective of sex, is the most effective at procuring food.

Male Cooper's Hawks do develop more rapidly than females and they leave the nest 2–4 days earlier than females (Meng 1951). This difference in development could be an adaptation to forestall any competitive advantage that larger females might possess (Newton and Marquiss 1979). Differential development, however, could occur for reasons other than intersexual competition. It might be, for example, that smaller size allows, rather than competitively compels, males to fledge sooner. Our data give no support for the existence of intersexual competition in nestling Cooper's Hawks. These results are consistent with those reported for other raptor species by Newton (1979).

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Diving rhythms and diurnal roosting times of Pelagic Cormorants.—Insight into the foraging ecology of diving birds such as cormorants may be gained by timing their diving sequences. In particular, the ratio of dive times to pause times (D/P) can reveal a species' physiological diving abilities (Dewar, The Bird as a Diver, Witherby, London, England, 1924; Dow, Auk 81:556–558, 1964). Possible differential physiological limitations may in turn explain the ecological separation of some cormorant species into shallow and deeper feeding zones (e.g., Stonehouse, Ibis 109:600–605, 1967). Other variables such as foraging success and the duration of foraging and diurnal roosting are useful in understanding variation in foraging behavior between species and among individuals of different ages within a species (Morrison et al., Wilson Bull. 90:414–422, 1978). Detailed observations of foraging have been made for only a few species of cormorants and the ways in which diving variables differ among species, age groups, and habitat types remain largely unknown. In this paper we present our findings on diving sequences and the intervals between bouts of feeding and diurnal roosting in Pelagic Cormorants (*Phalacrocorax pelagicus*). The data were obtained as part of a broader ecological study of this species in Barkley Sound, British Columbia.

Study area and methods.—From 1 July to 5 September 1982 and 1 July to 15 August 1983 we observed cormorants as they foraged near a diurnal roosting site off Taylor Island in the Deer Group Islands, Barkley Sound. The study site is typical of coastal habitat on the west coast of Vancouver Island (see Carter et al., Colonial Waterbirds 7:25–34). The bottom was rocky and water depth ranged from 0.5 to 20 m. Approximately 15 individuals, mostly immatures and non-breeders, regularly foraged in this area. We identified immature birds by their generally brown plumage and the lighter coloration of the breast and neck (see Palmer, Handbook of North American Birds, Vol. 1, Yale Univ. Press, New Haven, Connecticut, 1962). The exact age of the immatures was not known but they were likely in their first year because no young had yet fledged in either year from local breeding sites and because adult plumage is apparently acquired by the second year (Palmer 1962).

Dive and pause times were recorded with a stopwatch to the nearest sec from land 25 to 300 m from the birds. Pause times were recorded only when they were terminated by a dive and did not include periods after dives when prey was handled or birds swam to other foraging locations. Diving sequences of 10 or more dives were used in our calculations. We considered a foraging bird to be successful if it surfaced with prey in its bill; as this may not always be the case, our estimates of success are minimal. We calculated percent success only for complete foraging bouts. Length of the entire foraging bout was from the time the first dive began to the start of typical post-feeding behavior, e.g., vigorous plumage shaking, splashing, and often head dipping.

Birds were not marked, and thus, we could only occasionally record the time each spent roosting during the day between foraging bouts. In these cases we distinguished individuals by plumage characteristics (e.g., white flank patches), or by their position on the roosting site. Weather and tidal conditions were recorded during each observation bout, and water depth was estimated using hydrographic charts corrected for tidal level.

Results and discussion.—Seventy percent of the observed foraging sequences of adult and immature cormorants were in water 2–5 m deep, although birds sometimes foraged at depths down to 20 m. While prey may be encountered in the water column, we suspect that most of these dives were to the bottom. Robertson (Condor 76:346–348, 1974) reported that near Mandarte Island, British Columbia, Pelagic Cormorants fed mostly on prey characteristic of the littoral-benthic zone. Ainley et al. (Condor 83:120–131, 1981) reported that Pelagic Cormorants fed primarily on prey that "remain in close contact with, and even conceal

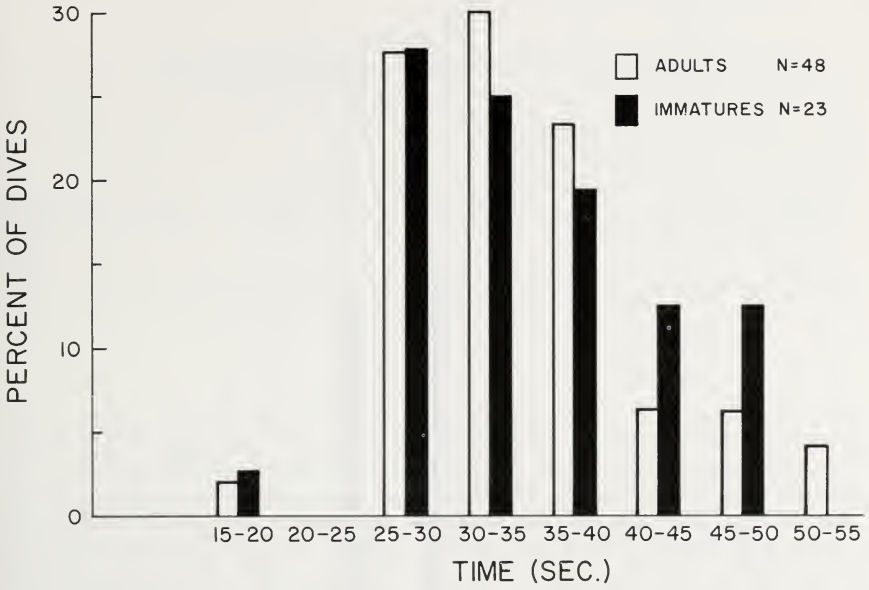

FIG. 1. Duration of dives of adult and immature Pelagic Cormorants in water 2–5 m deep.

themselves in, the rock and kelp substrate." Twice we identified prey as gunnel (Pholidae) and sculpin (Cottidae), both benthic fishes. Depths to 20 m are well within the physiological diving limits of this species (see Palmer 1962).

Diving sequences were recorded for 48 adults and 23 immatures foraging in water 2–5 m deep (these may include some repeat observations of the same birds). The distributions of diving times and pause times are given in Figs. 1 and 2, respectively. The mean diving time of adults (34.9 ± 4.1 sec, N = 1328) was significantly lower ($P < 0.05$, $t = 2.105$) than that for immatures (35.5 ± 7.8 sec, N = 474). We also found that the mean adult pause time (15.2 ± 3.2 sec, N = 460) was significantly lower ($P < 0.001$, $t = 5.76$) than that for immature birds (16.9 ± 3.9 sec, N = 190). Occasionally we were able to record pause time immediately following a measured dive time. For these paired values, the mean D/P ratio for adults foraging in water 2–5 m deep (2.3 ± 0.5, N = 390) differed significantly ($P < 0.001$, $t = 3.563$) from that of immatures (2.1 ± 0.7, N = 132). These D/P values nevertheless are sufficiently close to reveal similar diving abilities between these age groups (see Morrison et al. 1978).

Our D/P values agree closely with the value of 2.0 that Dow (1964) reported for a Pelagic Cormorant diving in depths between 1.5 and 6.1 m. Morrison et al. (1978) reported a D/P ratio of 2.1 for Olivaceous Cormorants (*P. olivaceous*) foraging in a shallow estuary and compared it to a value of 2.0 for Double-crested Cormorants (*P. auritus*) foraging in coastal waters. Stonehouse (1967) reported D/P ratios of 2.3–3.0 for four species of shags in New Zealand. Morrison et al. (1978) suggested that similarities in D/P ratios between various habitats and water depths indicates that the optimum diving rhythm among cormorant species is similar.

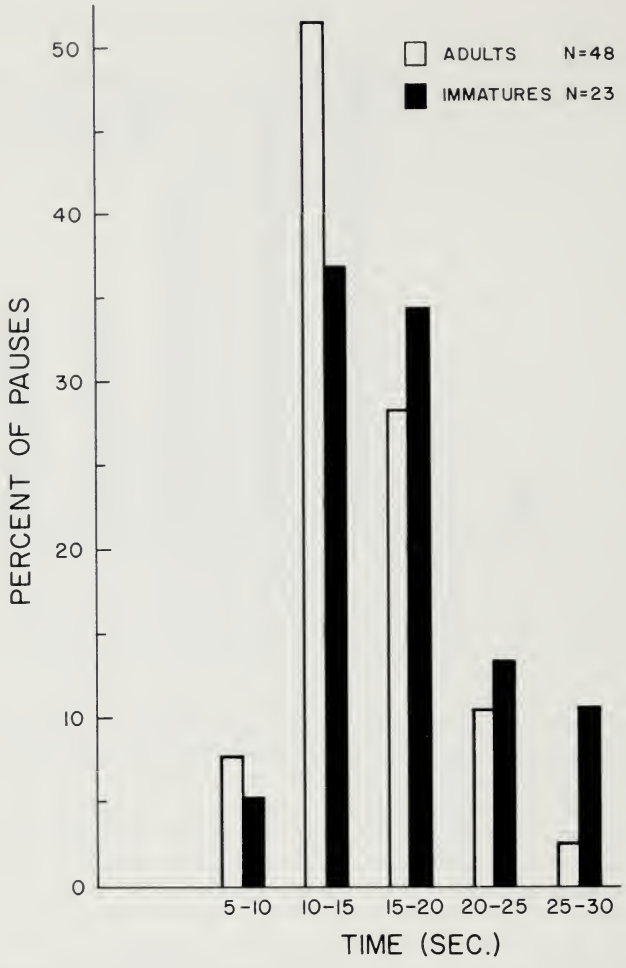

FIG. 2. Duration of pauses of adult and immature Pelagic Cormorants in water 2–5 m deep.

Water depth may be an important influence on the duration of dives and pauses (Simmons, Br. Birds 63:300–302, 1970; Batulis and Bongiorno, Auk 89:665–667, 1972; Morrison et al. 1978). Dewar (1924) and Stonehouse (1967) reported that the D/P ratios increase with depth to a critical value, and then fall as a physiological limit is reached. We observed that the D/P ratio for adults and subadult Pelagic Cormorants did not change significantly as depth increased to 20 m ($P > 0.05$, $t = 1.721$). This supports Dow's suggestion (1964) that if the dive and pause times are mainly functions of water depth, the D/P ratio for a species should remain approximately constant.

We found no significant difference ($P > 0.2$, $t = 0.063$) in capture rate for complete for-

TABLE 1

FORAGING AND DIURNAL ROOSTING TIMES FOR ADULT AND IMMATURE PELAGIC CORMORANTS

	Adult		Immature		
	$\bar{x} \pm SD$	N	$\bar{x} \pm SD$	N	
Foraging time (min)	25.9 ± 15.3	30	23.1 ± 15.8	15	$P > 0.2$, $t = 0.573$
Diurnal roost time (min)	86.0 ± 39.1	22	84.6 ± 32.7	15	$P > 0.2$, $t = 0.114$
R/F[1]	3.3		3.7		

[1] Ratio of time spent at diurnal roosting sites (i.e., out of water) to the time spent foraging.

aging bouts by adults (10.8 ± 8.4%, N = 30) and immatures (11.0 ± 13.3%, N = 16). Morrison et al. (1978) reported that Olivaceous Cormorants entering their first winter could dive as well as adults (as reflected by similar D/P ratios), but captured prey less successfully. They suggested that capture technique, maneuverability, and the development of a search image affect the capture rate of individuals of different ages. Our data indicate that in certain habitats Pelagic Cormorants can acquire adult diving ability and capture success by at least their first summer.

Adults and immatures had similar diurnal roosting and foraging times (Table 1). These values may be affected by environmental factors, which influence prey availability and capture rate, and by physiological factors. Rijke (J. Exp. Biol. 48:185–189, 1968) demonstrated that the physical structure of cormorant feathers renders them less water repellent than those of ducks. This may reduce buoyancy and enhance underwater feeding (Owre, Ornithol. Monogr. No. 6, 1967; but see Elowson, Auk 101:371–383, 1984). The increased wetability of cormorants and anhingas (*Anhinga* spp.) has led to speculation that wing drying may play a role in the spread-wing postures typical of this family (see Clark, Auk 86:136–138, 1969; Berry, Madoqua 8:5–55, 1976). Siegfried et al. (Zool. Afr. 10:183–192, 1975) suggested that poor water repellency impairs the birds' thermoregulatory properties and results in relatively short foraging bouts in non-breeding birds. Mahoney (pp. 461–470 *in* Proc. Symp. on Birds of the Sea and Shore, J. Cooper, ed., African Seabird Group, Cape Town, South Africa, 1979) further suggests that thermal physiology may influence species distribution. The ratio of time spent out of water to the time spent foraging (R/F) may thus be expected to differ between species and habitats. We recorded an R/F value of 3.3 for adult birds (Table 1). This value was 5.4 for adult Olivaceous Cormorants (calculated from the data in Morrison et al. [1978]) and 0.7–3.0 for four species of cormorants inhabiting freshwater and marine habitats in South Africa (calculated from data in Siegfried et al. [1975]). Our understanding of the factors affecting these R/F values is incomplete and the continued documentation of diving variables and diurnal roost times is needed to provide further insight into the ecology and physiology of these diving birds.

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Use of urban stormwater control impoundments by wetland birds.—This note reports marsh bird and shorebird use of different types of stormwater control impoundments in Columbia, Howard Co., Maryland. Mallard (*Anas platyrhynchos*) pair and brood use of these impoundments was reported earlier (Adams et al., Wildl. Soc. Bull. 13:46–51, 1985).

Detention and retention basins are used extensively in modern stormwater control. Detention basins are designed to hold water temporarily and release it slowly to a receiving body of water. They are usually dry or muddy between storms. Retention basins are designed to maintain a permanent water pool.

Study area and methods.—Columbia is located in the Piedmont Plateau physiographic region which is characterized by rolling hills with numerous stream valleys, many of them wooded. Soils in the area are strongly acidic with high available moisture capacity.

Thirty-four stormwater control facilities were studied during the spring and summer of 1982. The facilities included 3 lakes, 22 permanent water ponds, and 9 detention basins. Permanent water ponds were subclassified as deep (13 ponds) or shallow (9 ponds), and detention basins as located within or above stream bottoms. For further description of the study area see Adams et al. (Wildl. Soc. Bull. 12:299–303, 1984; 1985).

A standardized bird census was conducted at all basins twice per week from 1 March to 15 May 1982, and once per week from 15 May to 15 July 1982. Counts were made between 30 min after sunrise and 30 min before sunset, and they were allocated randomly among days of the week (Monday–Friday) and hours of the day. Each lake, pond, and dry basin was treated as a single sample unit. To facilitate data acquisition, lakes were divided into sectors which were numbered on maps for easy reference in the field. Sector observations were combined for each lake census.

The observer (LWA, LED, or TMF) slowly walked the perimeter of each pond, basin, and lake counting all marsh birds and shorebirds in the area. Data were recorded individually by pond, basin, and lake sector. The census was conducted when weather conditions provided good visibility, little or no precipitation, and light or no wind.

A bird-use index (UI) was calculated for each impoundment as:

$$UI=(F + N + I)/A$$

where:

F = percentage of censuses with ≥ 1 bird,
N = number of birds/number of censuses,
I = percentage of impoundments of each type used by birds,
A = impoundment size (ha).

The migratory bird UI was calculated with data collected during March–May and the breeding bird UI was calculated with data collected during June.

Results and discussion.—Use of detention basins by wetland birds was very low, a reflection of the unsuitability of such basins as habitat for these birds. Four Killdeer (*Charadrius vociferus*) and three Red-winged Blackbirds (*Agelaius phoeniceus*) were recorded during the study.

Spotted (*Actitis macularia*) and Solitary (*Tringa solitaria*) sandpipers, and Red-winged Blackbirds were the most common migrants using permanent water ponds and lakes (Table 1). The three species made up between 80 and 91% of the total wetland bird observations at these impoundments during migration. Several other wetland bird species were recorded during migration, but only the Red-winged Blackbird remained in substantial numbers during the breeding season (Table 1). It was found primarily at ponds. Lakes received very

TABLE 1

SPECIES COMPOSITION (%) OF MIGRATORY AND BREEDING MARSH BIRDS AND SHOREBIRDS AT PERMANENT WATER IMPOUNDMENTS, COLUMBIA, MARYLAND, 1982

Season	Species	Impoundment type		
		Shallow pond	Deep pond	Lake
Migratory (March–May)	Green-backed Heron	4.1	4.0	2.9
	Killdeer	3.6	0	4.6
	Common Snipe (*Capella gallinago*)	5.6	1.1	0.6
	Spotted Sandpiper	7.7	10.3	33.1
	Solitary Sandpiper	10.8	6.9	6.3
	Yellowlegs (*Tringa* spp.)	0.5	0	1.1
	Least Sandpiper (*Calidris minutilla*)	0	0	0.6
	Red-winged Blackbird	67.2	74.1	40.6
	Unidentified shorebird	0.5	3.4	10.3
	Total percent	100.0	99.8	100.1
	Total birds	195	174	175
Breeding (June)	Great Blue Heron	0	0	16.7
	Green-backed Heron	19.7	5.2	50.0
	Killdeer	1.5	0	0
	Red-winged Blackbird	78.8	94.8	33.3
	Total percent	100.0	100.0	100.0
	Total birds	66	97	6

little use by marsh birds and shorebirds during the breeding season. Only one Great Blue Heron (*Ardea herodias*), three Green-backed Herons (*Butorides striatus*), and two Red-winged Blackbirds were recorded at lakes during June.

During migration significant differences (Kruskal-Wallis test: $H = 12.0$, df = 2, $P < 0.005$) (Hollander and Wolfe, Nonparametric Statistical Methods, John Wiley & Sons, New York, New York, 1973) were noted in wetland bird use of impoundments. Multiple comparisons based on the Kruskal-Wallis test indicated differences (at an experimentwise error rate of 0.15) between shallow and deep ponds, shallow ponds and lakes, and between deep ponds and lakes. The median UI value for shallow ponds was 13.9 (range = 4.5–44.7, N = 9) compared to 4.3 for deep ponds (range = 1.5–16.8, N = 13) and 0.3 for lakes (range = 0.3–0.5, N = 3).

Significant differences (Kruskal-Wallis test: $H' = 9.3$, df = 2, $P < 0.01$) in use of Columbia's permanent water impoundments by wetland birds also were observed during the breeding season. The median UI value for shallow ponds was 17.2 (range = 3.7–66.3, N = 9) compared to 7.4 for deep ponds (range = 1.3–45.2, N = 13) and 0.1 for lakes (range = 0.1–0.2, N = 3). Multiple comparisons based on the Kruskal-Wallis test (at an experimentwise error rate of 0.15) indicated that shallow and deep ponds were used significantly more than lakes, but no significant difference in use was observed between shallow and deep ponds. Fewer species and total bird observations were recorded during the breeding season

than during migration, and variability was greater during the breeding season. These factors may have contributed to the lack of statistical significance between bird use of shallow and deep ponds during the breeding season.

Almost 80% of the shallow ponds contained sediment bars at stream inlet channels. Wetland birds made extensive use of the mudflats and shallow water edges associated with these sediment deposits. Only 15% of the deep ponds had sediment bars extending above the water surface. In addition, the gently-sloped sides of shallow ponds contrasted sharply with the steep-sided deep ponds and lakes and contributed to the increased wetland habitat value of shallow ponds. These features also were considered important in greater use of shallow ponds by mallard pairs and broods (Adams et al. 1985).

Implications.—Our data indicate that man-made wetland habitat can be created in urban areas in connection with modern stormwater management practices. There is public support in Columbia, Maryland for such effort (Adams et al. 1984), and guidelines for considering wildlife in the design of urban stormwater control facilities have been published (Adams and Dove, Urban Wetlands for Stormwater Control and Wildlife Enhancement, National Institute for Urban Wildlife, Columbia, Maryland, 1984). We encourage biologists to work closely with engineers, landscape architects, municipal and other governmental officials, planners, developers, and others to create and manage such habitat.

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Extra-pair feeding in Western Grebes.—Among grebes only the solitarily nesting Australasian Little Grebe (*Tachybaptus novaehollandiae*) breeds cooperatively (Lane, Sunbird 9: 2, 1978). I report here three observations of extra-pair feeding in Western Grebes (*Aechmophorus occidentalis*) and discuss the possible function of that behavior.

I observed with a 15–60× spotting telescope 75 pairs of colonially breeding, dark-phase Western Grebes for 275 h between 8 May and 14 August 1983. The colony was on Duck Lake, 15 km NW of Creston, British Columbia (49°14′N, 116°37′W). I determined sex by body and bill size (Palmer, Handbook of North American Birds, Vol. 1, Yale Univ. Press, New Haven, Connecticut, 1962). Hereafter, A-male and A-female refer to paired grebes; B-male refers to unpaired, "auxilliary" male grebes (sensu Emlen, pp. 245–281 *in* Behavioural Ecology, Krebs and Davies, eds., Blackwell Scientific Publ., London, England, 1978).

At 17:38 on 30 June an A-female took a 6-cm yellow perch (*Perca flavescens*) from a B-male and ate it while the A-male was diving. Between 17:39 and 17:58 the A-male captured 10 fish, ate one, and gave nine to the A-female who fed eight to a <7-day old chick. At 17:58 the A-male chased the B-male away. On 18 July I observed a pair of grebes with four, 3-week old young. At 16:08, while the A-male was sleeping, the A-female took a 6-cm yellow perch from a B-male and fed it to one of the young. At 16:09 the A-male awoke and the B-male moved away from the A-pair. At 16:15 the A-female received the B-male in a "ratchet-pointing" posture (sensu Nuechterlein and Storer, Condor 84:351–369, 1982). At 16:16 the A-male caught a 4-cm yellow perch and gave it to the A-female, which in turn fed

it to one of the young. At 16:17 the A-male chased the B-male. Again on 18 July between 17:40 and 19:40, I observed a pair of grebes with three, 3-week old young. At 18:27 the A-female chased a B-male. Between 18:29 and 19:31 the A-male captured 12 fish and took two feathers. The A-male ate five fish, gave three fish and the two feathers to the young, and gave four fish to the A-female; the A-female dropped one of these and gave the other three to the young. At 19:31, while the A-male was diving about 20 m from the A-female, the A-female took a 6-cm yellow perch from the B-male and fed it to one of the young. At 19:35 the A-male returned and gave a 4-cm yellow perch to the A-female. The B-male moved away from the A-pair when the A-male returned.

Without marked birds of known genealogy the significance of this behavior cannot be known, though two possibilities seem likely: (1) B-males may be related to one or both A-pair birds and are attempting to increase their inclusive fitness by enhancing the breeding success of their kin, or perhaps by gaining experience in rearing young, or both (e.g., Brown, Am. Zool. 14:63–80, 1974; Woolfenden, Auk 92:1–15, 1975). (2) B-males may be attempting to procure mates. White-fronted Bee-eater (*Merops bulockoides*) auxilliary males may also engage in attempted mate procurement (Emlen 1978). The second possibility is consistent with the observed aggressive behavior of A-males toward B-males.

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An auxiliary with a mated pair and food-caching behavior in the Fish Crow.—Auxiliaries or helpers are documented for many North American birds. Auxiliaries are especially frequent within the family Corvidae (Goodwin, Crows of the World, Cornell Univ. Press, Ithaca, New York, 1976; Brown, Ann. Rev. Ecol. Syst. 9:123–156, 1978; Verbeek and Butler, Ibis 123:183–189, 1981; Kilham, Florida Field-Nat. 12:25–31, 1984). Corvids are also known to cache food (Goodwin 1976; Roberts, Am. Nat. 114:418–438, 1979; Hewson, Br. Birds 74:509–512, 1981; James and Verbeek, Behaviour 85: 276–291, 1982; Kilham 1984). Neither helpers nor food caching have been documented previously for Fish Crows (*Corvus ossifragus*).

Evidence of an auxiliary.—Two pairs of Fish Crows nested 30 m apart in the crowns of tall (32-m) loblolly pines (*Pinus taeda*) in a small pine grove beside the Clemson University Cemetery, Clemson, South Carolina, in 1984. I watched one pair for a total of 50 hr from 12 April to 14 June. No crows were marked.

In Fish Crows only the female incubates and broods the young (Goodwin 1976). The male supplies the female with food during the period in which she is engaged in these activities. The pair was physically distinguished from a third individual (see below) by their glossier plumage, other plumage characteristics (e.g., missing right inner secondary of male), and by their behavior. In all observations described below, the pair and a third individual were seen at the same time.

While the female was brooding at 16:39 EST on 20 May, the male returned to the vicinity of the nest and a brief (2-sec) low intensity chase ensued between him and a second individual. The chase ended in a mutual display near the nest-tree. Both birds glided parallel to each other with neck and bill angled down about 45°, bodies drooped below the head and tail (which was slightly fanned), and the outer primaries slightly slotted. Ten minutes later, both birds perched on top of the nest-tree, 2 m above the nest while the female was still brooding.

The two birds then flew off together. The male was not seen to engage in mutual display with other Fish Crows or to tolerate them near the nest-site.

The next day at 16:27, the male and a second individual were observed together at a cache site on a horizontal dead limb 18 m above ground in a large deciduous tree 25 m from the nest where the female was brooding. The male chased the second bird from this cache site when the latter attempted to approach it again about 7–9 min later. This behavior was repeated several times. However, the male tolerated the second bird near the nest-site and they engaged only in low intensity chases as on the previous day. During the same period, the male vigorously chased several other intruding Fish Crows from the vicinity (<30 m) of the nest-site and cache site between 17:11 and 17:15 on 21 May. During these chases, the second bird fed the female at the nest once at 17:14.

The male and a crow other than his mate shared food at another cache site on 25 May. The cache was on a limb 20 m up in a tall pine 20 m from the nest. The male flew to this cache at 16:07 carrying an English muffin and called. A second crow left its perch 25 m away to perch beside the male and eat the proffered muffin. Prior and subsequent to this event the two birds engaged in calling bouts. The female was brooding at the time. At 17:30, the second crow again attempted to land at the pine cache site and gave a begging call, but did not receive any food from the male. On 11 June, when the nestlings were about to fledge, the male and female engaged in a calling bout when the latter was off the nest. At this time a third bird was within 2 m of the male. Also on 11 June, while the female was on the nest, the male and another crow returned to the nest. Although the observations described above indicate a third crow was tolerated by the pair, conflict occurred among these individuals as well. High intensity chases between the male and the third individual occurred frequently, particularly when the extra bird attempted to approach the nest, whether or not the female was on the nest. Although the extra crow was not marked, I have no evidence that more than one bird was involved as an auxiliary.

Brown (Am. Zool. 14:63–80, 1974) emphasized that retention of young in jays with social systems similar to Fish Crows may lead to communal breeding systems. The relatedness of the third individual to the nesting pair of Fish Crows is unknown. Fish Crows are short-distance migrants and are rare at Clemson during winter (H. E. LeGrand Jr., in litt.; pers. obs.). If the auxiliary was an offspring of the pair from the previous year, it must have returned from the wintering area (Good, Ph.D. diss., Ohio State Univ., Columbus, Ohio, 1952).

Food-caching behavior.—Interactions involving the auxiliary at two cache sites are described above. Most interactions at caches, however, were between the male and female. The male brought all the food to the cache sites. The food was always refuse, usually bread, and often in a bolus. Food was wedged into crevices of tree limbs or left lying exposed on limbs; many items were brought to the same cache. The pair fed at the cache site in a deciduous tree (see above) from 17:09 to 19:00 on 21 May. At that time, the male fed either alone or with the female. The female also fed at the cache after the male had left the area; the female occasionally flew to an adjacent tree to eat after first provisioning herself with food from the cache. Similar behavior was observed on 25 May from 15:30 to 16:45, when the mated pair fed at a cache site in a pine tree (see above). The male also left bread at other cache sites on other limbs of different pine trees, and the female fed at these, both when the male was present and absent.

Intraspecific defense of the cache sites, other than incidents involving the auxiliary, occurred at least six times. Two incidents of interspecific defense involving Blue Jays (*Cyanocitta cristata*) also occurred.

Food caching may allow the pair more flexibility in brood care, especially as a buffer against environmental variability such as short-term food shortages (cf. James and Verbeek

1982). In particular, the female benefits by feeding herself and her brood with cached food at the time of her choice, rather than being directly fed by the male. By providing food for the female at cache sites near the nest during the brooding period, the male probably reduces the time the nest is exposed and increases the time he spends near the nest feeding and is available for nest defense. The auxiliary I observed usually was barred from access to food caches.

Acknowledgments.—I thank M. W. Collopy and an anonymous reviewer for constructive comments.—Douglas B. McNair, *Dept. Biological Sciences, Clemson Univ., Clemson, South Carolina 29631.* (Present address: *Box 324, Dan Ross Rd., Six Mile, South Carolina 29682.*) *Accepted 10 Oct. 1984.*

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Clutch size increase and intraspecific brood parasitism in the Yellow-billed Cuckoo.—Two recent reports have documented an increased clutch-size in new world cuckoos (*Coccyzus*) as a probable response to a superabundant food resource (periodical cicadas in the Yellow-billed Cuckoo [*C. americanus*] Nolan and Thompson, Ibis 117:496–503, 1975; tent caterpillars in the Black-billed Cuckoo [*C. erythropthalmus*], Sealy, Condor 80:103–104, 1978). Additionally, Nolan and Thompson (1975) provided evidence of interspecific brood parasitism and other laying anomalies during these periods of abundant food. Previous observations suggest that behavior such as intra- and interspecific brood parasitism (Darwin, The Origin of Species, 6th ed., John Murray, London, England, 1872; Bent, Bull. U.S. Natl. Mus. 176:1–506, 1940; Nolan and Thompson 1975), varying clutch and egg-size (Bent 1940, Nolan and Thompson 1975), and asynchronous hatching and interrupted schedules of laying (Bent 1940; Hamilton and Hamilton, Proc. Cal. Acad. Sci. 32:405–432, 1965) are regular aspects of *Coccyzus* breeding biology. As these normally non-parasitic cuckoos are related to obligate brood parasitic species, such observations may provide important clues as to the factors responsible for the evolution of brood parasitism (Hamilton and Orians, Condor 67: 361–382, 1967; Payne, Ann. Rev. Ecol. Syst. 8:1–28, 1977).

Intraspecific brood parasitism may be documented by eggs appearing after a clutch appears to be complete (Nolan and Thompson 1975) by eggs within a clutch differing greatly in size, shape or coloration (Todd, Birds of Western Pennsylvania, Univ. Pittsburgh Press, Pittsburgh, Pennsylvania, 1940; Hamilton and Hamilton 1965; Nolan and Thompson 1975), or by examining egg proteins with electrophoresis (Manwell and Baker, Aust. J. Biol. Sci. 28: 545–557, 1975). Given cuckoos' unusual breeding habits, this latter method would seem to be the most reliable. Because proteins of undeveloped eggs are those of the mother alone, any protein polymorphism reflects (with high probability) the maternal genotype. If, therefore, different genotypes occur between eggs within a single nest it is very likely that two or more females contributed eggs to that nest (Manwell and Baker 1975; Yom-Tov, Biol. Rev. 55:93–108, 1980).

In this note we present observations made on the nesting of the Yellow-billed Cuckoo in eastern Kansas during spring and summer of 1981. The spring of 1981 was an emergence period for the 17-year periodical cicada (*Magicicada* spp., Brood XIV), and had abnormally high numbers of other insects (R. Holt, pers. comm.). Because of the prior report correlating cicada years with breeding anomalies in cuckoos, we attempted to determine whether 1981 clutch sizes were larger than those of previous non-cicada years, and whether intraspecific brood parasitism was occurring.

Methods.—We searched for nests in and around Lawrence, Douglas Co., Kansas, during the period 1 May–15 August 1981. After locating a nest, we revisited it if possible and recorded the order and dates of laying, the final clutch-size, and the fate of the nest. To

TABLE 1

ELECTROMORPH AT THE ESTERASE LOCUS, LENGTH, WIDTH, AND LENGTH/WIDTH FOR EACH EGG OF NEST A OF THE YELLOW-BILLED CUCKOO FROM DOUGLAS COUNTY, KANSAS

Egg #	Esterase electromorph	Length (mm)	Width (mm)	Length/width
1[a]	ss	28.5	24.6	1.16
2	ss	29.1	24.7	1.18
5	ss	29.5	24.9	1.19
3	ff	32.0	22.2	1.44
4	ff	33.2	23.1	1.44

[a] Egg numbers given arbitrarily.

compare clutch-sizes for 1981 to those of other years in the same general locality, we used nest-data card records from files in the Ornithology Division, Museum of Natural History, University of Kansas. We used only local nests where the observer noted that the clutch was complete, or the nest was followed by the observer past hatching. We also included seven clutches from a 1972 study in the same area (P. von Achen, pers. comm.; Fitch and von Achen, Kans. Ornithol. Soc. Bull. 24:12–15, 1973). If interrupted laying (Hamilton and Hamilton 1965) was overlooked, these data would be biased towards lower clutch-size. We have no reason, though, to believe that this was the case. We had no records from other years of periodical cicada emergence.

We collected two, five-egg clutches for electrophoresis. Egg white was removed from each egg and the relative amount of embryonic development was noted. We resolved esterases and general proteins on starch gels using a LiOH-borate buffer of pH 6.7 (Selander et al., Univ. Texas Publ. 7103:49–90, 1971). Egg length and width were measured, and a ratio of length to width was computed.

Results.—We found 10 nests between 1 June and 15 August 1981. Seven of these were found in June. Periodical cicadas emerged in early May, peaked in late May, and most were gone by mid-June. Thus, all of the cuckoo clutches were initiated after the peak of cicada abundance. Of six cuckoo nests that were followed to their end, five were depredated and one was blown from its tree. Mean clutch-size (3.80 ± 0.92 eggs, $N = 10$) was significantly larger than the mean clutch-size of 55 nest records (3.19 ± 0.87, $t = 2.02$, $P \leq 0.05$). Clutch-size was independent of date ($r = 0.05$, $P > 0.95$).

Both of the five-egg clutches had eggs in various stages of development. Clutch A had three eggs with small but various-sized embryos (eggs 1, 2, and 4; eggs were numbered arbitrarily), and two with relatively little development (eggs 3 and 5). Clutch B also had various stages of development. Yellow-billed Cuckoos generally begin incubation after laying their first egg. Thus, asynchronous development might be expected. We found no apparent electrophoretic differences between egg white from the developed and undeveloped eggs.

No polymorphism was detected on gels stained for general proteins. On gels stained for esterase, three presumptive loci were resolved. In clutch B no differences in electromorphs were evident. However, within clutch A locus 1 exhibited two morphs (designated here as putative genotypes ff and ss). Eggs 1, 2, and 5 were ss, eggs 3 and 4 were ff (Table 1). Considering that eggs 3 and 5 were undeveloped and that egg white proteins are of maternal origin (Manwell and Baker 1975), it is probable that eggs 1, 2, and 5 were from a female(s) different from the one which laid eggs 3 and 4. Even if these are embryonic genotypes, the

probability is very low ($\chi^2 = 5.4$, df = 2, $P = 0.07$) that a heterozygote cross, segregating under Mendelian laws, would result in these genotype frequencies.

The electrophoretic results, by themselves, cannot tell us whether more than two females laid the eggs, only that at least two females laid the eggs. However, the length and width of eggs 1, 2, and 5 were very different from those of eggs 3 and 4 (Table 1). Shape of the eggs, as the ratio of length to width, appears to be a stronger discriminator than average dimensions (Table 1). These results, combined with the electrophoretic results, suggest that a single female laid eggs 1, 2, and 5, and that a different, single female laid eggs 3 and 4.

Discussion.—Our data suggest a positive reproductive response to a periodical cicada eruption (as in Nolan and Thompson 1975). This suggests that when a female cuckoo obtains excess food she can increase her clutch-size. For cuckoos, which sometimes have difficulty finding their uncommon food (Bent 1940, Hamilton and Hamilton 1965), such plasticity may be of considerable adaptive value.

Nolan and Thompson (1975) found that nesting anomalies occur with greater frequency during years when extra food resources are available. While we have no data with which to compare years, the anomalies reported here did occur during the period of cicada emergence. Cuckoos have long been supposed to be intraspecifically brood parasitic (Bent 1940, Hamilton and Hamilton 1965, Nolan and Thompson 1975); above we presented evidence which supports this view. Manwell and Baker (1975) and Gowaty and Karlin (Behav. Ecol. Sociobiol. 15:91–95, 1984) also used electrophoretic data to detect intraspecific brood parasitism in House Sparrows (*Passer domesticus*) (where nearly 10% of the clutches examined were of mixed motherhood) and in Eastern Bluebirds (*Sialia sialis*), respectively. From our limited sample of clutches we cannot assess the frequency of such parasitism, or its impact on the host or parasite's reproductive success.

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Bathing behavior of Purple Martins.—A description of Purple Martin (*Progne subis*) bathing behavior is given in Bent (Life Histories of North American Flycatchers, Larks, Swallows, and Their Allies, Dover, New York, New York, 1963:429) from observations made by Audubon: "They are very expert at bathing and drinking while on the wing, when over a large lake or river, giving a sudden motion to the hind part of the body, as it comes into contact with the water, thus dipping themselves in it, and then rising and shaking their body like a water spaniel, to throw off the water."

In August 1980 I observed bathing behavior of Purple Martins near a roost in Ann Arbor, Washtenaw Co., Michigan. Martins arriving in the area prior to entering the roost perched on utility wires 150–200 m away from the site. Martins bathed in a waste water lagoon (ca 0.6 ha) 20–50 m from the utility wires. Martins that were engaged in bathing activity flew from the wires to a height of 2–6 m above the water surface and circled for 30 sec to 3 min before making first contact with the water. After bathing, the birds flew back to the wires

to ruffle their feathers and preen. Bathing activity by a small number of birds attracted others, which resulted in groups of 40 or more circling the lagoon, most in a counterclockwise direction. As this behavior took place over an extended period each day (19:00–20:50), it is likely that newly arriving martins joined in the bathing activity as others left. My observations show the following sequence of events for each "water contact": (1) the martin flies just above the water surface; (2) brakes slightly by spreading and dropping the tail; while (3) raising the wings to about a 45-degree angle; (4) the forward motion carries the bird onto the breast which "bounces" on the surface showering water onto the back and wings; (5) the bird immediately regains flight speed and flies upward until; (6) reaching a safe height (about 2–4 m) to shake off excess water. Step 6 may not be performed until the bird is wet enough to have water streaming from the plumage; thus, a number of water contacts may occur before shaking takes place.

A bathing episode, timed from first to last contact with the water's surface, is a series of "contacts." The shortest episode was 10 sec with one contact and the longest was 1 min 31 sec with eight contacts ($\bar{x}$ = 46 sec, SD = ±27, N = 13), although one martin had 10 contacts in 1 min 22 sec. The most common number of contacts was three ($\bar{x}$ = 4.2, SD = ±6.5, N = 13), representing 61.5% of the observations. The contact rate for the combined observations was one contact for every 10 sec.

I observed a male martin scratching its neck while gliding overhead. This activity proceeded as described by Goodwin (Auk 76:521–523, 1959) for the Bank Swallow (*Riparia riparia*), "While gliding, the head was lowered and turned to the side while the foot was brought forward beneath the wing." This behavior has not been previously described for this species, but has also been observed by C. R. Brown (pers. comm.) for *P. subis* at his study sites in Texas.

Acknowledgments.—I would like to thank R. Storer and C. R. Brown for reading and commenting on a previous draft of the manuscript.—Richard A. Wolinski, *2450 Baker Rd., Dexter, Michigan 48130.* *Accepted 1 Nov. 1984.*

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First breeding record of the Snow Bunting for British Columbia.—The breeding range of the Snow Bunting (*Plectrophenax nivalis*) in North America encompasses arctic habitats from northern Ellesmere Island south to southwestern Alaska and extreme northwestern British Columbia (Am. Ornithol. Union, Check-list of North American Birds, 6th ed., Washington, D.C., 1983). No verification of breeding in British Columbia, however, has previously been published. We reviewed 16 summer records including the first known breeding of this species in British Columbia. All records are from two mountainous areas, extreme northwestern British Columbia, generally referred to as the Haines Triangle, and the vicinity of Mount Edziza/Spatsizi Plateau, about 540 km to the southeast of the first area.

Haines Triangle.—This area is about 150 km northwest of Haines, Alaska, and includes the southern St. Elias Mountains. Snow Buntings were first noted in summer in the province near Mile 60 on the Haines Road by C. J. Guiguet (B.C. Prov. Mus., pers. comm.) on 8 July 1956. On 8 July 1958, R. B. Weeden (Can. Field-Nat. 74:119–129, 1960) collected an adult female in breeding condition in the same area and indicated Snow Buntings were probably breeding nearby. Then in the summer of 1980, a party from the British Columbia Provincial Museum (BCPM) obtained a series of adults and immatures (BCPM 16680–15594) near 1525 m in mountains near Mile 91, along the Haines Road. Two fledglings, obtained on 2 July, 1980, with traces of natal down (BCPM Photo No. 877—see Campbell

and Stirling, Syesis 4:217–222, 1971), represent the first breeding record for the province. The same summer on 10 July, above 1800 m in the Datlasaka Range west of Mile 73, a brood of four recently fledged young with two parents was found foraging among boulders in a bare scree area; also on 10 July a bulky nest of grass, lichen, and moss, containing five large, feathered young was found in a vertical rock crevice below an overhanging patch of snow. No adults were at the nest, but a male, presumably a parent, was nearby. Five adults, without young, were also seen foraging at the edges of melting snow fields nearby.

We are aware of five other summer records of adults in the Haines Triangle. Immediately west of the Datlasaka Range, near Shini Lake, J. M. Cooper and M. McNall (B.C. Prov. Mus., pers. comm.) watched two adult males fighting on 16 June 1983 and 17 km to the south the senior author observed an adult male feeding with Rosy Finches (*Leucosticte arctoa*) near Samuel Glacier Mountain on 28 June 1983. Farther west, on an unnamed mountain north of Tats Lake (59°37′N, 137°44′W), D. W. Nagorsen (pers. comm.) noted flocks of up to 12 adults from 9 to 15 July 1983 above 1490 m. No immatures were noticed and one adult male (BCPM 17860) was collected (testes 9 × 5 mm [left] and 7 × 5 mm [right]). The other two records were both east of Haines Road. On 6 June 1978, a pair was seen at Tina Creek (Blood and Chutter, 1978 Raptor Nesting Survey for Shakwak Highway Improvement Project, Thurber Consultants Ltd., Victoria, British Columbia, 1978) and on 12 July 1975, Claire Kooistra (pers. comm.) counted 10 adult Snow Buntings with a flock of Lapland Longspurs (*Calcarius lapponicus*) feeding in Chilkoot Pass.

Mt. Edziza/Spatsizi Plateau.—On 21 July 1982, E. Edie, D. Humphries, A. Harestad, and B. Van Drimmelin (pers. comm.) observed four adult Snow Buntings in moraine deposits above tundra on the south and west sides of Mt. Edziza. The three summer records from the Spatsizi Plateau were in mountainous areas from 1800 to 1000 m in elevation. On 7 June 1976, six adults were recorded south of Hyland Post, and single adults were seen at Stalk Lake on 10 July 1976 and Klahowya Lake on 17 July 1976 (Osmond-Jones et al., Spatsizi and Tatlatui Wilderness Parks, British Columbia Provincial Parks Branch, Victoria, British Columbia, 1977).

The Snow Bunting probably breeds regularly in appropriate habitat in alpine areas above 1500 m in the Haines Triangle area. It is a common breeder along the coasts of Alaska (Kessel and Gibson, Status and Distribution of Alaska Birds, Stud. Avian Biology No. 1, 1978) and is considered an "uncommon breeder or probable breeder" in the mountains around Alaska, 110 km south of the British Columbia breeding locations. Farther inland, in the vicinity of Mt. Edziza/Spatsiza Plateau the Snow Bunting is probably a rare summer resident although breeding is yet to be confirmed.

Acknowledgments.—The authors extend their thanks to those mentioned for permission to incorporate their observations in this paper. A. J. Erskine, W. E. Godfrey and J. C. Barlow provided editorial comments.—R. Wayne Campbell, *Vertebrate Zoology Division, British Columbia Provincial Musuem, Victoria, British Columbia V8V 1X4, Canada* and Brigitta M. Van Der Raay, *Center for Quantitative Studies, Univ. Washington, HR-20, Seattle, Washington 98195.* *Accepted 3 Oct. 1984.*

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ORNITHOLOGICAL LITERATURE

THE A.O.U. CHECK-LIST OF NORTH AMERICAN BIRDS, 6th Edition. By The Committee on Classification and Nomenclature of the American Ornithologists' Union. A.O.U., 1983:877 pp. $35.00 ($28.00 to A.O.U. members).—Weighing in at 1317 grams (virgin copy with only the protective covering removed) and 877 pages, the long-awaited permutation of the "chiseled in print" decisions of the A.O.U. Check-list Committee, the 6th Edition has arrived. Over 20 years in preparation, the maroon-bound tome contrasts in more than weight and length with the familiar blue-bound 5th Edition (1071 grams and 691 pages, in a respectfully handled, but not abused, 21 year old copy).

As befitting the importance of this publication, and appropriate for the product of a committee, the Auk (101:625–636, 1984) wisely chose a spectrum of voices to review the 6th Edition. This reviewer has refrained from reading those reviews and now adds his independent—and opinionated—view.

Each edition of the Check-list has covered a slightly different geographical area depending on the dominant personality of the preparing Committee. The 6th Edition omits Greenland and includes Hawaii. However, to this reviewer, the fundamental error in concept for this edition, made prior to the participation of most of the members that actually produced the Check-list, was the decision, certainly fostered by Eugene Eisenmann, to have the check-list area extended south to the Panama–Colombia border. Thus, the less well known (in currently published literature) distributions of birds in Mexico, Pacific Guatemala and Honduras, and Caribbean Nicaragua are combined with the well-defined distributions of birds in North America, Costa Rica, and central Panama into a hodgepodge of distributional validities, with the inexperienced having to accept it all at the same value. Still, the distributions are as good as the Committee could make them with the assistance of numerous (acknowledged) ornithologists who reviewed draft copies of the manuscript. Unfortunately, in part beyond the fault of the Committee, reviewers were not necessarily those with the most knowledge of the regions involved.

Because of the vast increase in the number of species included, size and time dictated that subspecies not be included. This is, in fact, a blessing in disguise. We do not have voted decisions on subspecific concepts from a committee, with few exceptions, without taxonomic experience.

My second major complaint—and it is inherent in the committee system—is the lack of attribution. Thus, the eminently admirable and useful addition of "Notes" for many species present amorphous committee decisions. If individual authors had initialed a given note one could judge its acceptability. Or, with a reference, have the basis for evaluating that decision. Still, when the Committee could not gird up its collective belt and make the "right" decision (for example, to recognize all "quack-quack" ducks as the same species), it at least acknowledged its ambivalence by providing the Notes—and we thank it for that. Thomas Howell is to be congratulated on the extended (20 vs 6 pages) and edifying Preface. Four useful appendices provide annotated lists of: A) species recorded only on the basis of sight records, B) species included on the hypothetical list of the 5th Edition but not now accepted, C) forms of doubtful status or hybrid origin, and D) introduced species or escaped birds that have not become established. A list of A.O.U. numbers for species concludes the text. A hundred grams of bibliography would have added immeasurably to the Check-list.

Aside from the deletion of subspecies, the greatest changes in the 6th Edition, for readers less familiar with current systematics, are taxonomic levels at which many groups are recognized; the amplification of subfamilial names; and the rearranged order of some pas-

serine groups. Three examples: flamingos (*Phoenicopterus* spp.) were elevated to ordinal rank; most 9-primaried oscine families were reduced to subfamilies; and Ploceidae was fractured into three families, with other groups separating them. These changes reflect, in part, the current ferment in avian classification, a near war zone of conflicting concepts based on custom, and revived and productive old and, most dramatically, new technologies. It is a difficult period in which to teach avian taxonomy, but an exciting one for the science. We do thank the Committee for not following the "crows-last" nonsense of the Peters world check-list. And I briefly note the unique Roman enumeration of the orders in the Table of Contents.

I expect more fevers have been caused by some of the English (I refrain from using the word *Common*) names the Committee settled for, rather than any of the other (and far more important) aspects of the Check-list. The concept of a single, world-wide common name per species is a laudable one, but the monikers resulting from the Committee's deliberations are less so. Each of us will have his or her pets but "Green-backed" instead of Striated Heron, and "Chihuahuan" instead of American White-necked Raven are outstanding flubs. Fortunately, we are not forced to follow, and although editors may get tired of inserting alternate names in parentheses, we can continue to use names that make common sense. At least a few (too few) of the long used geographical and respected patronymic names were restored.

I would like to see future Check-lists issued in a looseleaf format. Hopefully in the not too distant future the Check-list will be on a centralized computer. It will be updated on an ad hoc basis by experts on given taxa, and revised sections will be available by printout through our individual institutional facilities. In the meantime every administrator involved in ornithology will have the 6th Edition on his desk. I expect every scientist will also retain that spot for his well-worn blue-bound edition.

Finally, it must be stated that some of the finest ornithologists in North America served on the Committee, a thankless job in my opinion, and devoted uncountable hours to produce this Check-list. Burt L. Monroe, Jr. especially deserves our highest respect—his organizational and administrative capabilities and steely strength were instrumental in the completion of this effort.—Robert W. Dickerman.

Tropical Seabird Biology. By Ralph W. Schreiber (ed.). Studies in Avian Biology, No. 8, Cooper Ornithological Society, 1984:114 pp., 46 figs., 52 tables. $12.00—This volume of six papers is a product of a symposium that was conducted at an annual meeting of the Pacific Seabird Group in Honolulu, Hawaii, on 2 December 1982. The objectives of the symposium were to bring together a group of seabird biologists that had worked on tropical species and to explore the differences in biology between warm-water and temperate- or cold-water species. The logistical task in assembling biologists with such expertise was formidable, given the global scale of tropical seabird studies: Ascension Island, the Galapagos Islands, Christmas Island (Pacific and Indian Oceans), the Hawaiian Islands, and the Seychelle Islands. This volume represents the first attempt to synthesize our knowledge of the biology of tropical seabirds since the classic monograph by Ashmole and Ashmole (Comparative Feeding Ecology of Seabirds of a Tropical Oceanic Island, Peabody Mus. Nat. Hist., Yale Univ. Bull. 24, 1967). The publication is professionally produced by the Cooper Ornithological Society and admirably edited by R. W. Schreiber. It is inspirational to see a symposium proceeding produced barely one year after its occurrence.

The volume begins with a contribution by Ainley and Boekelheide that compares regional avifaunas in the Pacific. Using a series of cruises that passed through tropical, subtropical, subantarctic, and Antarctic waters, the authors attempt to locate avifaunal boundaries and

to characterize seabird communities. They find the most important boundaries to be the Equatorial Front (23° isotherm) and the pack ice edge, with the Subtropical and Antarctic Convergences being less effective boundaries. The authors continue the earlier work by Ainley on the use of different feeding techniques in various communities. These authors show that seabirds in all oceanic ecosystems in the Pacific tend to feed in the morning and evening. In addition, they show that tropical waters have the strongest tendency for species to associate in multi-species feeding flocks, which prompts them to encourage a detailed study of the interaction between seabirds and schools of tuna.

A. W. Diamond's "Feeding overlap in some tropical and temperate seabird communities" complements earlier studies that have focused on ecological segregation among coexisting species. Using his own data from the Seychelle Islands and published data from the North Sea and Christmas Island (Pacific), he finds prey size to be only weakly correlated to predator size and suggests that a bird's foraging strategy is as good an indicator of prey size as the bird's body size. Most significantly, Diamond finds tropical seabirds that feed offshore to have diets so similar that they overlap as much as 90%. In contrast, species that feed inshore have less overlap and greater dietary diversity. Although these data do challenge traditional competition theory, Diamond's argument would be more convincing if it were possible to identify flying fish and squid in seabird stomachs past the family level. These prey families are the source of much of the dietary overlap that he cites, and each is represented by numerous species in tropical waters. Tropical seabirds may, in fact, consume very different proportions of the various species within these families.

G. C. Whittow provides an excellent summary of the factors that affect gas and heat transfer between an egg and its microclimate. Comparing tropical seabirds with those from higher latitudes, prolonged incubation in tropical species has necessitated substantial adaptations in the physiology of eggs and embryos. For example, the rate of gas transfer across the eggshell is relatively low in all tropical seabirds. Whittow demonstrates the importance of pipping for tropical species, a time when much of the total water loss and oxygen uptake by the egg occurs. He also summarizes studies of heat transfer between parents and the egg and metabolic studies that imply that even the northernmost "tropical" seabirds do not require the generation of additional heat for incubation purposes.

N. P. Langham compares clutch size, brood size, and growth rates among four North Sea and four tropical Australian terns. His data demonstrate the tendency for temperate terns to lay more eggs, raise more young, and fledge chicks faster than tropical species. He considers the various growth strategies with respect to semi-precocial development of young and the ability of tropical chicks to withstand long periods without food. Perhaps the most interesting aspect of this paper is the anomalies presented by Black-naped Terns (*Sterna sumatrana*). Although restricted to tropical waters in the Pacific and Indian Oceans, Black-naped Terns resemble temperate species by having multiple-egg clutches and a fast-growth strategy for chicks.

R. E. Ricklefs presents the results of a model of the energetics of breeding seabirds that matches the energy requirements of reproduction to the ability of parents to transport energy from their feeding areas to the colony. His results confirm biological intuition by predicting energy requirements to be greatest during chick brooding. Ricklefs believes that brood size may be limited by the mass of food that parents can carry in flight. He suggests several fruitful avenues of study, including meal size, feeding rates, and the biochemistry of prey consumed by young.

This volume concludes with J. B. Nelson's "Contrasts in breeding strategies between some tropical and temperate pelecaniforms." Nelson effectively synthesizes a vast amount of information, demonstrating the rare ability to reason inductively as well as deductively. He explores a complex suite of breeding adaptations that influences the breeding strategy of

each species and, in theory, produces the greatest number of young at least cost. His detailed comparisons between temperate and tropical pelecaniforms include breeding frequency, age of first breeding, timing of breeding, clutch size, composition of breeding cycle, attachment to breeding area, and social characteristics of breeding groups.

This volume is of interest to any ornithologist or ecologist, and is essential for those who specialize in seabirds. Its only shortcoming is its length, which was limited primarily by funds. Unfortunately, the lead agency of the federal government for marine birds, the U.S. Fish and Wildlife Service, would not fund travel or publication costs of this symposium. The study of marine birds is poorly funded because their life cycle, being partly terrestrial and partly pelagic, falls in the jurisdictional cracks between the Department of the Interior (a terrestrial agency) and the National Oceanic and Atmospheric Administration (NOAA, an oceanic agency). One cannot help but believe that were NOAA given responsibility for the study and management of these creatures, future symposia, such as this, would be properly funded, attract a high proportion of the experts on the subject, and the scientific product would be enhanced.—Craig S. Harrison.

Iowa Birds. By James J. Dinsmore, Thomas H. Kent, Darwin Koenig, Peter C. Petersen, and Dean M. Roosa. Iowa State University Press, Ames. 1984:356 pp., 132 range maps, 1 numbered text fig., numerous black-and-white photographs, 1 table. $27.95.—More than most states, Iowa has been fortunate in having good faunistic works on birds, including an excellent state journal (Iowa Bird Life), for much of the 20th century. This most recent addition seems a worthy descendent of the line of Anderson (1907), DuMont (1933), and Brown (1971), to mention only the most notable compilers of the state's bird data. The 5 authors of the present work were, in essence, members of a committee that divided the project mainly along taxonomic lines, each member covering certain families or orders of birds in the state. Each of the authors has years of experience (e.g., Petersen 34, Kent 35) doing field work on Iowa birds. The organization is fairly traditional for a state bird book, with chapters or sections on the geography and geology of Iowa, its topography and natural regions, on the history of the bird work, and on the terminology used in the book. Nomenclature and order of species is essentially as in the 6th Check-list of the American Ornithologists' Union (1983). The book is not actively taxonomic in nature. Subspecies are not mentioned.

Most (280 pages) of the book is given to well-annotated species accounts where all species are listed in appropriate sequence. At the beginning of each Family there is a summary of the number of species occurring world-wide, and/or in North America, and in Iowa, plus brief natural history notes on the group. The individual species accounts are concise and clearly written using both abbreviated and complete sentences. The general status (abundance and seasonal occurrence) of the species in Iowa is given first, followed by more detailed information under headings of: Habitat, Spring Migration, Summer, Fall Migration, Winter, and Comment. Under "Comment" a wide range of subjects are considered, including numbers of birds and changes thereof, plus special notes on breeding, distribution, identification, history, etc. Especially for less-common species, a map showing the known Iowa distribution is provided. Many of the species accounts include 1 or more special references, in addition to a list of more general references at the end of the book.

The use of code designations in the species accounts for classes of records (e.g., Class IV = hypothetical, Class V = insufficient evidence to judge the record) seemed rather a waste of effort to me. The status of each species is explained perfectly well in English, and the code does not seem to add anything. The authors have provided extreme migration dates for most species as the earliest (latest) 3 records—a sound policy—to give an idea of the range

in variation. A number of the species accounts include fine (but small) photographs of birds—many by Fred W. Kent. One of the most interesting and potentially useful features of the accounts is the banding data of Petersen, an extraordinary bander (80,000 birds, 1958–1981). To make the data more useful, however, more details on effort are required, and I hope that a detailed report on Petersen's study is to be published.

The authors have been conservative in accepting records—in some cases perhaps too cautious (I suspect that both *Anthus spragueii* and *Calcarius pictus* are regular transients in Iowa, and both so distinctive in behavior as to be identified easily). If the authors were cautious about their official list, in the overall (annotated) list they wisely presented the available information for future students to consider.

In an appendix that follows the species accounts, there are separate listings (without annotation) of the state's 362 species (188 breeding, plus possibly 4 others) according to status, including lists entitled "regular" (276 species), "casual" (16), "accidental" (62), "extirpated" (6), and "extinct" (2). At the end of Chapter 1 it is noted that the Great-tailed Grackle (*Quiscalus mexicanus*) and Vermilion Flycatcher (*Pyrocephalus rubinus*) were found in Iowa in 1983—perhaps too late for the publication. As the flycatcher is not in the annotated list, the total number of species should be 363 as suggested on page 3. These numbers do not include 12 "hypothetical" species, which in the authors' view are probably correct records, or 26 species judged to be probably incorrect records, but all—including the 26—are in the annotated list.

When one thinks of the stretches of prairie and the marshes that once typified Iowa, it is hard to accept that the Greater Prairie Chicken (*Tympanuchus cupido*) is essentially extirpated, and that the Northern Harrier (*Circus cyaneus*) and King Rail (*Rallus elegans*) are now rare. "Iowa Birds" is a good reference. Its information should be used in the struggle for better conservation.—Richard R. Graber.

The Marine Ecology of Birds in the Ross Sea, Antarctica. By David G. Ainley, Edmund F. O'Connor, and Robert J. Boekelheide. Ornithological Monographs No. 32, American Ornithologists' Union, Washington, D.C. 1984:x + 97 pp., 42 text figs. $9.00 ($8.00 to A.O.U. members).—Seabirds are mysterious. They roam over vast stretches of ocean, occurring in great abundance in some areas and avoiding others. Until recently, marine biologists rarely have been able to do much more than note their broad distributional patterns from ships-of-opportunity, hoping that revelation might eventually arise from masses of data.

This study represents a major step forward. It is based on six cruises in the Ross Sea in the austral summers of 1976–1980 and represents the first systematic survey of the area's seabirds. Working from Coast Guard icebreakers, Ainley, O'Connor, and Boekelheide used strip-transect methods to determine the density of seabirds. They also gathered oceanographic data (ice cover, sea surface temperature, salinity, vertical temperature profile) relevant to understanding bird distribution. From these data—and previous detailed knowledge of the fauna—they were able to compute population sizes of birds on the open sea, estimate their ranges, and evaluate factors influencing their distribution.

The size of bird populations in the Ross Sea, one small sector of the Antarctic, are impressive: Emperor Penguin (*Aptenodytes forsteri*), 342,000; Adelie Penguin (*Pygoscelis adeliae*), 2,249,000; Antarctic Petrel (*Thalassoica antarctica*), 5,000,000; Snow Petrel (*Pagodroma nivea*), 2,000,000; South Polar Skua (*Catharacta maccormicki*), 18,500. Cape Pigeons (*Daption capense*), on the other hand, were almost absent from the area (21 sightings

in 6 cruises). While astronomical numbers of seabirds are not news, the estimate of the Antarctic Petrel population is truly impressive, because there are no known colonies that could account for so large a population. How refreshing that many mysteries of the austral regions remain to be solved.

But how good are the population estimates? Their validity depends on many factors, of which the most important is maintaining a constant width to the transect strip. This is difficult on the open sea, but pack ice conditions make for a stable platform and thus consistency in the determination of the strip. Other potential problems include the propensity of certain species to approach or to avoid ships, and the differences in the attractiveness of various types of ships. By working only from icebreakers, the latter problem was minimized. The problem of attraction, however, remains. While encounters with penguins are likely to be unbiased, ships in the Antarctic are so few that they certainly attract some species, perhaps from very long distances. In my experience, Snow Petrels, Antarctic Petrels, and skuas are the most curious, and this behavior can lead to greatly inflated values of their abundance. The censusing techniques used by Ainley et al. partly compensate for this problem, but it never goes away. The test of the estimates, however, comes in comparing ship-based figures with those made from land-based studies. In some cases (e.g., South Polar Skua), the agreement is surprisingly good, which gives credibility to estimates of less-studied species. Additional verification and testing are needed.

Analyses of the distribution of individual species revealed much about their preferences for specific oceanographic conditions. Pack ice is a requisite for some, open water for others, while the Antarctic Slope Front affects both the distribution and pelagic range of many species. Observations also indicated the existence of an unknown colony of Emperor Penguins near King Edward VII Peninsula. Limited but important collecting provided new information on the distribution of breeding vs nonbreeding individuals and their respective ranges from presumed colonies. Additional analyses clarified the composition of seabird communities.

The research program was well-conceived and well-executed, and the monograph is crammed with information that will be useful to anyone studying pelagic birds. And if there are lapses in writing ("This was one of the most ubiquitous species. . . . It was observed almost everywhere" [p. 37]), they do not detract from the monograph.

For those whose interest is less specialized, read at least two short sections that bear on current issues in conservation. The first, Community Biomass (pp. 78–81), deals in part with alleged competition between seabirds and marine mammals, and the oft-repeated tale that depletions in stocks of baleen whales have allowed a compensatory increase in krill-eating penguins and seals. This idea has been accepted uncritically by an embarassing number of biologists, and has been recounted so often in the popular press that it has taken on the aura of fact. Ainley et al. kindly prick the balloon of belief, pointing out that the assumption on which the idea is based—that Antarctic populations of birds and mammals are food-limited—is unproved and unlikely. The complementary section on Trophic Interactions (pp. 81–86) is equally interesting, for the authors conclude that krill may be far less important in seabird diets than we have been led to believe. These findings have major implications, and they point out the need for long-term scientific studies—and a healthy dose of critical thinking—before political solutions to "managing" the continent's resources are devised.

I suspect that the monograph will become the standard against which future distributional and ecological studies of seabirds will be measured. It is the excellent product of many more years of hard work by Ainley and his colleagues than the Methods section can indicate.—J. R. Jehl, Jr.

Biology of the Peregrine and Gyrfalcon in Greenland. By William A. Burnham and William G. Mattox. Meddelelser om Grønland, Bioscience 14, 1984:25 pp., 12 figs., 12 tables. Dkr. 46.75 excl. of VAT and postage.—This paper presents the results of 10 years of study (1972–1981) in western Greenland that took place primarily in the region of Søndre Strømfjord. The study is still ongoing. Many of the data were hard won, especially in the early years. Frequently the researchers had to make week-long treks with 25–35 kilos of gear in backpacks just to gather data on 2–3 eyries. I still have vivid memories of trudging over the landscape with the survey crew in 1975; backpack so heavy and feet so sore I could hardly walk after a one week trek. Over 40 researchers were involved in data gathering and 9 organizations provided some support. Within this report the bulk of the data deals with the Peregrine Falcon (*Falco peregrinus*). Of the 17 pages containing biological data, 9 were devoted to peregrine biology, 3 to the Gyrfalcon (*Falco rusticolus*) and the remaining 5 to such topics as migration, banding recoveries, chemical pollutants, and interspecies competition. Both species behave as they do elsewhere in their circumpolar ranges with but a couple of exceptions. The 2 species were not found to occupy the same cliff simultaneously (except in 1984). The authors attempt to explain why this would have developed in the historic sense. The authors speculate that the distribution of nests of the Common Raven (*Corvus corax*), which Gyrfalcons usurp for nesting, and food availability have been important factors in the dispersion of the 2 species.

A second departure from general peregrine biology concerns food habits. While peregrines are noted for their catholic diets this was not the case in Greenland. Four species made up about 90% of the peregrine diet in 1973. This probably results from the fact that there just are not large populations of many species to prey on at inland localities. In some ways it is disappointing that so much data were lost by not checking food remains in eyries more thoroughly. For all years of the study, productivity was recorded at each eyrie and in most cases young were banded. Data on food, however, were only reported for 1973. Why weren't food remains systematically collected while in each eyrie? Had such data been collected a better idea of regional food differences, yearly prey fluctuation, and biomass consumption at each eyrie may have emerged. Overall, considering the physical and logistic restraints encountered by field parties, this study is a credit to the authors and an important addition to raptor biology.—Clayton M. White.

The Winter Exploitation Systems of Bay-breasted and Chestnut-sided Warblers in Panama. By Russell Greenberg. University of California Publications in Zoology, Vol. 116. Berkeley, 1984:x + 107 pp., 20 black-and-white figs. $7.50.—How do the sympatric species of a large genus such as *Dendroica* divide up their mutual habitat? Such workers as MacArthur and Morse have offered solutions to this problem for the breeding season that have been widely accepted, but we know much less about the situation on the wintering grounds. A concurrent question concerns the interaction of these migrants with the resident species. To obtain some enlightenment on these matters, Greenberg elected to study the Bay-breasted (*D. castanea*) and the Chestnut-sided (*D. pensylvanica*) warblers. These species are largely allopatric during the winter, but their ranges do overlap slightly in Panama. One can take exception to the author's statements that these two species are closely related and are morphologically and ecologically similar, but the results of his study are of great interest.

The two species differ almost completely in their winter exploitation systems. The Chestnut-sided Warbler is largely solitary, and defends small territories around the territories of antwrens, with whose flocks it commonly associates. It forages on the undersides of leaves in the mid-level of the trees and seldom resorts to frugivory. On the other hand, the Bay-

breasted Warbler often occurs in small groups, but less often is in mixed-species flocks. It rarely defends territories and does not associate with antbird flocks as much. It is much more of a generalist in its choice of foraging substrate and foraging strata than is the Chestnut-sided Warbler. The Bay-breasted Warbler also feeds on fruit perhaps as much as 20–25% of the time. Greenberg relates the difference in foraging substrate to behavior during the breeding season. The Chestnut-sided Warbler in its breeding range feeds largely on broad-leaved trees where the richest source of arthropods is the underside of the leaves. On the other hand, the Bay-breasted Warbler feeds in conifers during the summer, and typically conifer-feeding birds use the top of the branches. In the tropics, species that feed on the upper surfaces of the leaves typically become more omnivorous since the upper surfaces are not as rich in food as are the undersides.

Bay-breasted Warblers are about 25% heavier than Chestnut-sideds. Previous studies by Greenberg have shown that large warblers, such as the Bay-breasted, Cape May (*D. tigrina*), and Yellow-rumped (*D. coronata*), tend to feed on the upper surfaces, and that small species such as the Chestnut-sided, Magnolia (*D. magnolia*), and Black-throated Blue (*D. caerulescens*) feed on the undersides.

Greenberg speculates that feeding on the underside of leaves makes an individual more vulnerable to predators, and that possibly for this reason the Chestnut-sided Warbler associates more commonly with antwrens, taking advantage of their warnings of the presence of predators.

Bay-breasted Warbler populations in Panama show a steady decline as the winter season progresses, but this is not observed with Chestnut-sideds.

This is a well executed study, and the report which is packed with good data should be read by all warbler aficionados as well as ecologists.—George A. Hall.

The Ecology of a Summer House. By Vincent G. Dethier. University of Massachusetts Press, Amherst, Massachusetts, 1984:133 pp., 6 line drawings. Cloth $15.00, paper $7.95.—This delightful little book is something of a tour de force. The author, Vincent Dethier, sets out to demonstrate the depth of ecology and behavior that can be illustrated by the inhabitants of one small summer house in Maine. The reader is introduced to, among others, a field cricket (*Acheta pennsylvanicus*) singing on the hearth, Cliff Swallows (*Hirundo pyrrhonota*) constructing mud nests on the chimney, deer mice (*Peromyscus maniculatus*) breeding in the living room sofa, orb spinners (*Araneus trifolium*) building intricate webs between the rafters, a spotted salamander (*Ambystoma maculatum*) sheltering in the root cellar, and little brown bats (*Myotis lucifugus*) roosting under the eaves. Dethier does not stop with descriptions of what is found where, but goes on to detail fascinating observations and experiments on the natural history of these creatures. Dethier is a distinguished ethologist and physiologist, as well as being the author of several, fine earlier works of popular science (e.g., the extremely amusing "To Know A Fly"). The breadth of Dethier's biological knowledge, his fine prose style, and his sweet-tempered outlook combine to make the present work special.—William A. Searcy.

Roger Tory Peterson at the Smithsonian. By Richard L. Zusi. Millpond Press, Venice, Florida, 1984:72 pp., 55 color plates, 67 black-and-white illustrations. $9.95 + $1.50 postage. (Available from Smithsonian Institution Press, P.O. Box 1579, Washington, D.C. 20013.)—In honor of the fiftieth anniversary of the first publication of the "Field guide to the birds" the Smithsonian Institution arranged a retrospective exhibition of Roger Peterson's work over the years. We have here the catalog of that exhibition held in the spring of

1984. Richard Zusi selected a wide variety of paintings representing the various aspects of Peterson's art. Thus, in addition to field guide type paintings and drawings, we have examples of his illustrations of various books, of the Wildlife Stamps, and of his large bird portraits. Admirers of Peterson will welcome this collection which has been excellently reproduced by the Millpond Press. It is an illuminating experience to see how much better these reproductions are than were the ones in the various Field Guides. For example, compare the plate of large shorebirds on page 127 of the 1980 Guide with its counterpart on page 63 of this catalog to gain a new perspective on Peterson's work.

The text contains a small amount of biographical information and a discussion of the origin and evolution of the Field Guide concept. There are a few photographs of the artist at work and a few of his excellent color photographs of birds.—George A. Hall.

Working Bibliography of the Golden Eagle and the Genus *Aquila*. By Maurice N. Le Franc, Jr., and William S. Clark. Scientific and Technical Series No. 7, National Wildlife Federation, Washington, D.C., 1983:234 pp., $14.95.—This is the third contribution in the bibliographic series of the Raptor Information Center of the National Wildlife Federation. The text begins with a fine forward, by the late Leslie Brown, that introduces the user to the genus *Aquila*. In addition to a master list of 3459 literature citations, this book earns its title of "working bibliography" by including a brief introduction to the ecology and taxonomy of these eagles, a permuted list of keywords (defined in an appendix), a species and a geographic index of citations, and a list of citations of occurrences. Most of the North American literature and the major foreign journals were searched for titles up to and including September 1982. The number of citations per species is: Golden Eagle (*A. chrysaetos*)—2305, Lesser Spotted Eagle (*A. pomarina*)—632, Greater Spotted Eagle (*A. clanga*)—428, Tawny Eagle (*A. rapax*)—285, Steppe Eagle (*A. nipalensis*)—310, Imperial Eagle (*A. heliaca*)—468, Wahlberg's Eagle (*A. wahlbergi*)—167, Gurney's Eagle (*A. gurneyi*)—18, Wedge-tailed Eagle (*A. audax*)—86, and Black Eagle (*A. verreauxi*)—172.

The authors and the National Wildlife Federation should be commended for producing another valuable, easy to use, and intelligently produced bibliography. I highly recommend it for all libraries, public and private. The bibliography can be obtained from the National Wildlife Federation, 1412 16th St., Washington, D.C. 20036.—Gary R. Bortolotti.

INFORMATION FOR AUTHORS

The Wilson Bulletin publishes significant research and review articles in the field of ornithology. Manuscripts are accepted for review with the understanding that the same or similar work has not been and will not be published nor is presently submitted elsewhere, that all persons listed as authors have given their approval for submission of the ms, and that any person cited as a personal communication has approved such citation. All mss should be submitted directly to the Editor.

Text.—Manuscripts should be prepared carefully in the format of recent issues of The Wilson Bulletin. Mss will be returned without review if they are not properly prepared. They should be neatly typed, double-spaced throughout (including tables, figure legends, and "Literature Cited"), with at least 3-cm margins all around, and on one side of good quality paper. Do not use erasable bond. **Mss typed on low-quality dot-matrix printers are not**

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Tables.—Tables are expensive to print and should be prepared only if they are necessary. Do not repeat material in the text in tables. Tables should be narrow and deep rather than wide and shallow. Double space all entries in tables, including titles. Do not use vertical rules. Use tables in a recent issue of the Bulletin as examples of style and format. Tables should be typed on separate unnumbered pages and placed at the end of the ms.

Figures.—Illustrations must be readable (particularly lettering) when reduced in size. Final size will usually be 11.4 cm wide. Illustrations larger than 22 × 28 cm will not be accepted, and should be reduced photographically before submission. Legends for all figures should be typed on a separate page. Photographs should be clear, of good contrast, and on glossy paper. Drawings should be in India ink on good drawing board, drafting paper, or blue-lined graph paper. All lettering should be done with a lettering instrument or adhesive transfers. Do not use typewriter or computer lettering. Designate the top of each illustration and label (on the back in soft pencil) with author's name, ms title, and figure number. Submit two duplicates or readable xerographic copies of each figure as well as the original or high-contrast glossy photo of the original.

Style and format.—Recent issues of The Wilson Bulletin should be used as a guide for preparing your ms; all mss must be submitted in that format. For general matters of style authors should consult the "CBE Style Manual," 5th ed., Council of Biology Editors, Inc., Bethesda, MD, 1983. Do not use footnotes or more than two levels of subject subheadings. Except in rare circumstances major papers should be followed by a summary, not to exceed 10% of the length of the ms. Summaries should be informative rather than indicative, and should be capable of standing by themselves. Most units should be metric, and compound units should be in one-line form (i.e., $cm\text{-}sec^{-2}$). The continental system of dating (19 Jan. 1950) and the 24 hour clock (09:00, 22:00) should be used.

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Nomenclature.—Common names and technical names of birds should be those given in the 1983 A.O.U. Check-list (and supplements as may appear) unless justification is given. For bird species in South America not occurring in the area covered by the A.O.U. check-list (1983, 6th ed.) the Bulletin uses the common names appearing in Meyer de Schauensee "The Species of Birds of South America," 1966. Proper common names of birds should be capitalized.

The Editor welcomes queries concerning style and format during your preparation of mss for submission to the Bulletin. KEITH BILDSTEIN, EDITOR.

ANNOUNCEMENTS

INTERNATIONAL CODE ON ZOOLOGICAL NOMENCLATURE

The International Commission on Zoological Nomenclature has indicated that the 3rd edition of the International Code of Zoological Nomenclature will soon be available. The book consists of parallel English and French texts, totaling about 320 pages (216 mm × 318 mm). It will be for sale for 15 pounds, plus 1.50 pound for postage and handling, through the Publications Sale, British Museum (Natural History), Cromwell Road, London SW7 5BD, England. Individuals and organizations may also purchase it for $21.50, postage and handling included, through the American Association for Zoological Nomenclature, Room W-115, National Museum of Natural History, Washington, D.C. 20560.

In order that the Code will be widely available, a prepublication price of $18.75, postage and handling included, for individuals is in effect until March 31, 1985. Delivery of the Code will be in spring 1985. Checks drawn on a United States bank or International Money Orders should accompany all U.S. orders! Please make checks payable to American Association of Zoological Nomenclature.

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In anticipation of the 100th anniversary of The Wilson Ornithological Society, The Wilson Bulletin will publish a series of lists compiled by John L. Zimmerman of the past and present officers and Council Members of the Society. Below is a list of the Presidents of The Wilson Ornithological Society.

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Membership inquiries should be sent to Dr. Richard Stiehl, Department of Biology, Southeast Missouri State Univ., Cape Girardeau, Missouri 63701.

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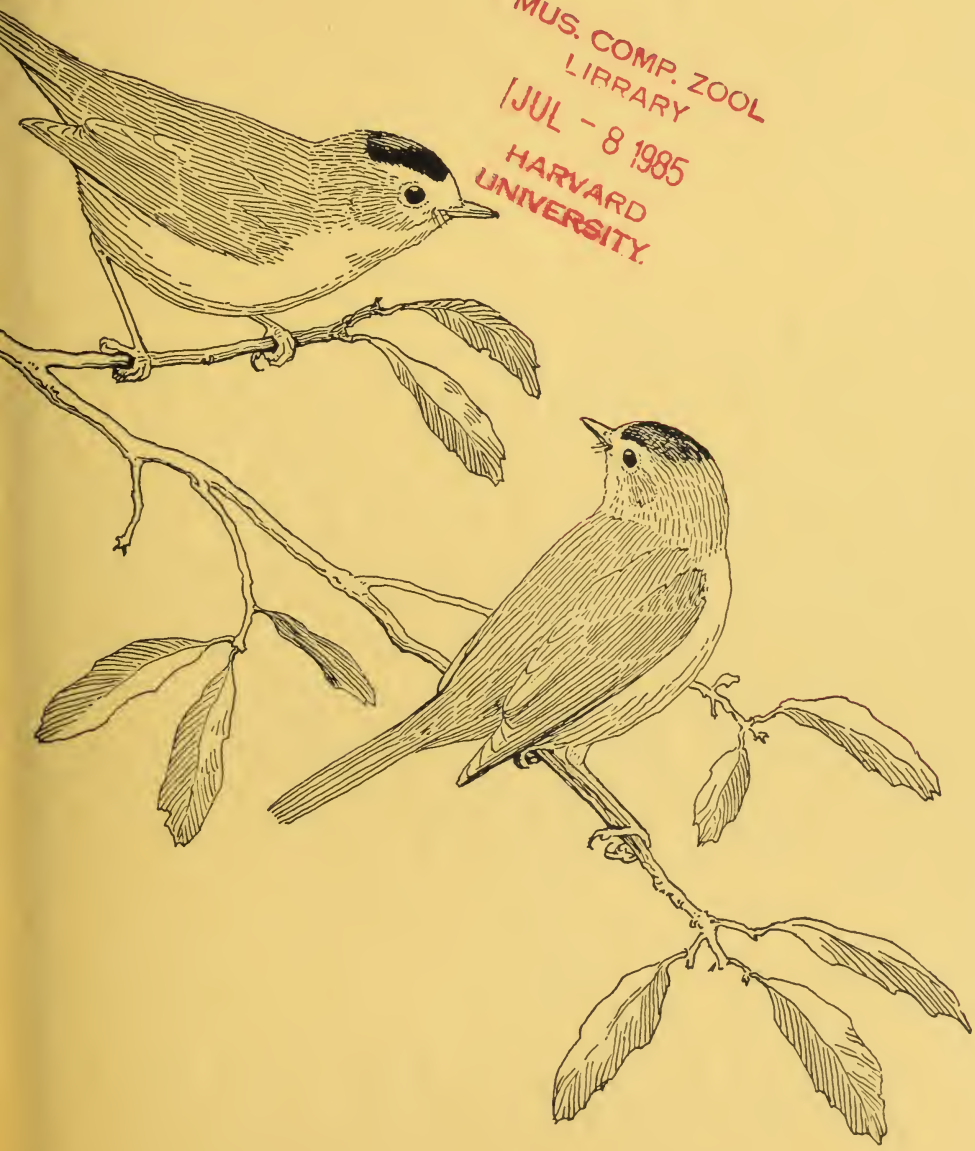

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Male Ornate Hawk-Eagle *(Spizaetus ornatus)*
at a nest, Tikal, Guatemala, April, 1979.
Photo by Albert Kuhnigk.

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OBSERVATIONS ON NESTING ORNATE HAWK-EAGLES IN GUATEMALA

BRUCE LYON AND ALBERT KUHNIGK

The Ornate Hawk-Eagle (*Spizaetus ornatus*) is a small eagle that inhabits the tropical rain forests from central Mexico to northern Argentina. Almost nothing is known of its breeding behavior, although 4 nests have been reported previously (Russell 1964, Brown and Amadon 1968, Kiff and Cunningham 1980). Here we present descriptions of 2 new nest sites and the first observations of the breeding biology of this species.

STUDY SITE AND METHODS

We observed nesting Ornate Hawk-Eagles at Tikal National Park in the Department of Petén in northeastern Guatemala. On 9 March 1977 we found an occupied hawk-eagle nest (nest A), but were unable to make detailed observations at the site. In March 1979 we returned to the site and found that the nest had fallen, and that there were no hawk-eagles in the immediate area. On 1 April 1979 we found a new nest (nest B), about 5 km from the old site. From 8 to 10 April we constructed a blind in the nest tree, 10 m from the nest. During this time, the incubating female hawk-eagle was very tame and remained on the nest while we worked in the tree. We started observations on 11 April and watched the nest for about 9 h each day until 27 April, resulting in a total of 170 h of observations.

The habitat at Tikal is a semi-deciduous, dry, tropical forest (Holdridge 1957). The most abundant tree species include zapote (*Acras* sp.), ramon (*Brosimum alicatrum*), mahogany (*Swietenia macrophylla*) and Spanish cedar (*Cedrela mexicana*) (Smithe 1966). Most of the rain falls during the wet season that lasts from May to November (mean annual rainfall of 1400 mm). The park is in a region of very low, eroded limestone hills, and surface water is limited to a few, widely scattered, small forest ponds where runoff collects. These "aguadas" are important watering holes for local wildlife. A more detailed description of the vegetation and climate at Tikal is provided by Smithe (1966).

NEST SITES

Nest A was 20 m up in a 30 m silk cotton tree (*Ceiba pentandra*). It was wedged into a fork of a large side branch, 5 m out from the trunk. Although the tree was an emergent, the nest was slightly below the canopy.

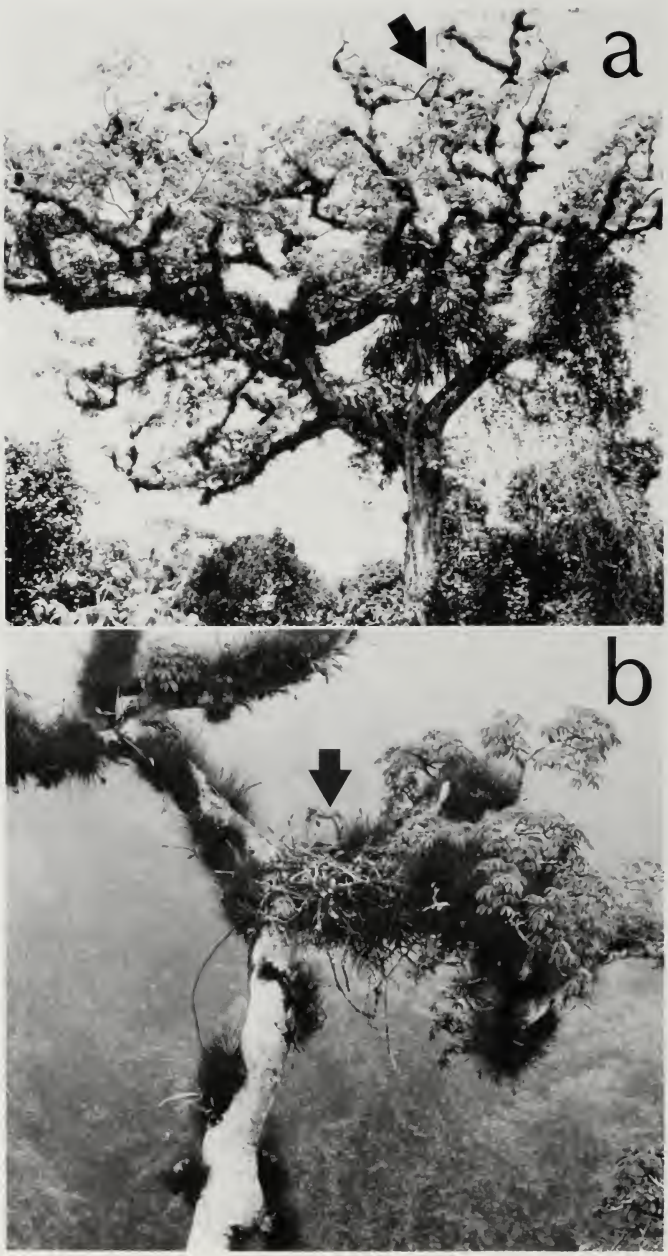

FIG. 1. (a) Giant silk cotton tree used for nesting by pair B in 1979. Arrow indicates position of nest, which is obscured from view by foliage. (b) Nest B in a fork of a side branch near the top of the tree. Arrow indicates nest position.

FIG. 2. Female at nest B during one of her breaks from incubation.

Nest B (Fig. 1) was 26 m up in a huge 30 m emergent silk cotton tree, well out from the main trunk near the end of a large side branch. The nest was 5 m above the top of the canopy, and its location afforded a clear view of the surrounding forest. The nest was roughly oblong in shape and was made of sticks between 5 and 10 mm in diameter. It measured 125 by 85 cm across and was 50 cm deep. When we climbed to the nest on 6 April it contained a single white egg, spotted with small faint brownish-red blotches. This is in contrast to the unspotted bluish-white eggs laid by a captive female (Kiff and Cunningham 1980), the only other egg description for this species.

Both Tikal nests were in tall emergent trees whose branches were well-festooned with a dense growth of bromeliads (Bromeliaceae). These bromeliads were likely incidental features of the nest sites, as the upper

branches of many emergent trees in the region are similarly covered with these epiphytes. We are aware of only two other descriptions of Ornate Hawk-Eagle nest sites. A nest in Panama was 28 m up in the crotch of a 31 m cativo tree (*Prioria* sp.) (Brown and Amadon 1968), and a nest in Oaxaca, Mexico, was in a crotch of the main trunk of a huge pine tree (L. Kiff, pers. comm.; data from R. Galley).

INCUBATION BEHAVIOR

The female performed 95% (121 of 126.6 h observed) of the incubation during the last two weeks of incubation (Fig. 2). The male provided the female with prey during this period and normally incubated only while she fed on this prey away from the nest. Normally, one member of the pair was at or very near the nest, and the nest was left unattended for only 9 min during the 127 h of observations during incubation.

During each daily 9-h observation period the female took an average of 11.4 short breaks (SD ± 2.73, range 7–13, N = 14) from incubation to preen, exercise, roll the egg, and collect leafy green sprigs for the nest bowl. These breaks averaged 3.5 min (SD ± 1.87, range 1–11, N = 128), and the female remained on the nest unless sprigs were collected.

The female collected leafy sprigs for the nest bowl at least once a day and always before 08:00. Twenty of the 22 sprigs the female brought to the nest came from a single tree 100 m NE of the nest tree. The female never collected sprigs from the nest tree itself. We observed the female collecting sprigs twice—on both occasions she flew to the end of a branch and removed a sprig with a couple of good tugs with her bill. She usually carried the sprigs to the nest in her bill (N = 6), but twice she used her feet. Preening was often associated with sprig-collecting, and often occurred in her "preferred" sprig-tree.

The male visited the nest daily, except on two occasions when he was absent for 1 and 2 d respectively. He always arrived before 12:00. He brought prey to the female on 6 of 9 visits, and prey transfers took place several hundred meters from the nest, and never at the nest. After the prey was given to the female, the male flew to the nest to incubate and he always left the nest upon the female's return. He usually incubated for 0.5 to 1 h, but one unusually long bout lasted 2 h when the male came to the nest without prey and the female presumably went off to hunt for herself. The male also collected leafy sprigs for the nest bowl, usually during breaks in his incubation bouts. Four of eight sprigs he collected were from the tree preferred by the female.

The prey provided by the male appeared to comprise almost all of the female's food during incubation. Only once during our observations did the female leave the nest area long enough to have been hunting.

HATCHING, CHICK DEVELOPMENT, AND NEST FAILURE

The day before the egg hatched the female began to incubate with her wings out and tail spread, similar to her brooding behavior after the egg hatched. At 08:00 on 25 April, the female returned to the nest with the remains of a Plain Chachalaca (*Ortalis vetula*) that she received from the male. This was the first time we observed prey brought to the nest. At 10:10 when the female rolled the egg, the blunt end fell off and the head and one wing of the chick emerged. Ten minutes later the chick was completely free of the shell. The female then ate most of the soft membranous tissue adhering to the shell. Several times during the day the female picked up and dropped the eggshell until it had been reduced to several large fragments. These fragments remained in the nest bowl.

By 12:20 the pure-white down of the chick was completely dry. When 2 d old, the chick could hold its head up long enough to be fed. By the third day it could maneuver itself to defecate over the edge of the nest cup. During the mornings of the second and third day the female brooded the chick with her wings and tail spread. On both days it was hot enough by 11:00 that she stood above the chick to provide shade.

On 27 April the female behaved abnormally and flew off the nest, leaving the chick exposed to the sun. The chick moved toward some shade but became caught in debris and died after 20 min of exposure to the sun, apparently of heat prostration. Prior to leaving the nest, the female was salivating heavily and thrashing her head about the nest. This behavior may have been a result of the exceptional heat that day. It is also possible that the female ingested and was stung by one of the large ants (*Paraponera* sp.) that were numerous on the branches of the nest tree. (One of us who was stung by an ant felt that it was easily as painful as a bee sting.)

The adult hawk-eagles remained in the vicinity of the nest after the chick's death and continued to bring leafy sprigs to the nest bowl. No observations were made after 29 April.

FOOD

We identified 5 prey items at the nest before the chick died; a young tinamou (Tinamidae), a Plain Chachalaca, a young Crested Guan (*Penelope purpurascens*), a Gray-headed Dove (*Leptotila plumbeiceps*) and a leaf-nosed bat (Phyllostomatidae). During incubation, the male brought the female a large whitish bird, but the prey was transferred too far away for identification. Kilham (1978) observed an Ornate Hawk-Eagle at Tikal attempt to catch a Crested Guan, and Brown and Amadon (1968) noted that medium- to large-sized birds and mammals as large as the kinkajoo (*Potus flavus*) are included in the diet.

NEST DEFENSE AND RESPONSE TO INTRUSIONS NEAR THE NEST

As hatch approached, the female began to attack us as we climbed to the blind, and only our vigorous waving and shouting prevented her from striking us. On the two occasions that the male was incubating when we arrived at the nest, he did not attempt to defend the nest in any way. At a nest in Oaxaca, Mexico, where the female had been collected before the nest was discovered, the male actively defended the nest against a climber (L. Kiff, pers. comm.).

On 16 March 1977 a troop of Spider Monkeys (*Ateles paniscus*) passing through the forest canopy passed within 25 m of nest A. The female hawk-eagle left the nest and swooped at one of the monkeys twice. The monkey responded by shrieking loudly and vigorously shaking the branch it was on before retreating into the foliage. On 6 April 1979 a troop of Spider Monkeys passed through the treetops within 20 m of nest B and although the incubating female watched them, she remained on the nest.

As hatching neared at nest B, the incubating female responded to raptors that soared within several hundred meters of the nest by raising her crest, mantling the egg, and calling loudly. Black Vultures (*Coragyps atratus*), King Vultures (*Sarcoramphus papa*), Turkey Vultures (*Cathartes aura*), Swallow-tailed Kites (*Elanoides forficatus*), and Black Hawk-Eagles (*Spizaetus tyrannus*) all elicited a calling response from her, the intensity depending on their distance.

NESTING PHENOLOGY

Incubation and fledging periods are not known for any *Spizaetus* eagle. *Hieraaetus* eagles, which are closely related to *Spizaetus,* have incubation periods ranging from 42 to 45 d, and fledging periods from 55 to 80 d (Brown and Amadon 1968). Using these data and extrapolating from hatch, the egg in nest B was probably laid during the second week in March and, had the eaglet survived, it would have fledged in late June or early July. Thus, the egg was laid in the dry season, and the chick would have been 3 weeks old when the wet season started. Most species of birds at Tikal begin to breed in early to mid-April (pers. obs.). Breeding in hawk-eagles at Tikal may be timed so that eggs hatch at the onset of the flush of young birds that takes place in late April and throughout May.

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helpful suggestions. We dedicate this paper to George Miksch Sutton, whose writings first encouraged us to go to the tropics.

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COLOR PLATE

The Frontispiece of the Ornate Hawk-Eagle (*Spizaetus ornatus*) has been made possible by an endowment established by George Miksch Sutton (1898–1982).

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A MODEL OF ENERGY CONSUMPTION IN BALD EAGLES: AN EVALUATION OF NIGHT COMMUNAL ROOSTING

George P. Keister, Jr., Robert G. Anthony, and H. Richard Holbo

Bald Eagles (*Haliaeetus leucocephalus*) are found only in North America and are associated primarily with coastal estuaries, inland lakes, and rivers throughout their range. In fall and winter they migrate from northern areas of harsh climate to coastal or southern areas with milder climates and more readily available food. They often concentrate in areas where food resources are plentiful, particularly in conjunction with anadromous fish runs or large concentrations of waterfowl. In these areas (e.g., Glacier National Park, McClelland 1973; Klamath Basin, Keister 1981), Bald Eagles frequently use night communal roosts with as many as 400 individuals on a given night. Similar behavioral patterns have been described for American Robins (*Turdus migratorius*) (Walsberg and King 1980), Red-winged Blackbirds (*Agelaius phoeniceus*) (Meanley 1971), nuthatches (*Sitta* spp.) (Kilham 1971), finches (*Lecosticte* spp.) (French 1959), Eastern Bluebirds (*Sialia sialis*) (Frazier and Nolan 1959), Common Grackles (*Quiscalus quiscula*) (Meanley 1971), and European Starlings (*Sturnus vulgaris*) (Francis 1976).

The adaptive significance of communal roosting in birds is not well understood, although a number of hypotheses have been proposed. One hypothesis assumes that selection of communal roosts with more favorable microclimates than surrounding areas aids in thermoregulation and energy conservation. Kelty and Lustick (1977) reported that European Starlings selected favorable microclimates provided by pine woods and thereby reduced daily existence metabolism by 12 to 38%. Likewise, Stalmaster (1981, 1983) found that Bald Eagles near the Nooksack River in Washington conserved energy by roosting in coniferous forests as compared with deciduous riparian areas. In contrast, Walsberg and King (1980) found that such behavior by the American Robin produced only a slight thermoregulatory benefit. They suggested that the thermal significance attributed to selection of nocturnal roosts in other studies (see Calder 1973, Calder and King 1974, Kelty and Lustick 1977) may not be applicable to most species and settings.

In this study, we developed a mathematical model of energy metabolism for Bald Eagles on the basis of microclimatic conditions in 4 communal roosts. This model was used to answer the following questions: (1) Do

communal roosts have more favorable microclimatic conditions than general local conditions? (2) Do communal roosts in the same general locality have different microclimatic conditions? (3) What is the energetic advantage, if any, of communal roosting? In addition, we asked which factors were most important in determining use of roosts by Bald Eagles.

STUDY AREA

The Klamath Basin is located in southcentral Oregon and northern California and is bordered by the Cascade Mountains to the west, the Fremont Mountains to the east, and the Medicine Lake Highlands to the south. Climate of the Klamath Basin is determined by elevation (~1250 m) and prevailing winds from the Pacific Ocean. The area has a mean annual precipitation of 36.3 cm with 70% falling between October and March, of which a large portion is snow. Mean monthly maximum temperatures range from 29.0°C in summer to 3.6°C in winter. Mean monthly minimum temperatures range from 10.9°C in summer to −6.0°C in winter (U.S. Dept. Commerce 1969). Natural vegetation changes with increasing elevation from grass-to-shrub to tree-dominated communities.

Three major Bald Eagle feeding areas and five communal roosts were located in the southern portion of the Klamath Basin. Feeding areas were associated with flooded areas on the basin floor and roosts were located 6–20 km from feeding areas on forested land at 1400–1950 m in elevation. The vegetation of four roosts was dominated by ponderosa pine (*Pinus ponderosa*); the other roost was in a mixed-conifer forest. A more detailed description of forest stand characteristics and roost trees is presented by Keister and Anthony (1983).

MATERIALS AND METHODS

Microclimate instrumentation and data collection.—Instruments were placed at each of four roost sites to measure air temperature, windspeed, solar radiation, and net radiation. Data were collected throughout most of the winter of 1979–80. In addition, regional weather data were obtained from Kingsley Field in Klamath Falls located on the floor of the Klamath Basin (U.S. Air Force and National Weather Service data).

A Thermilinear Thermistor (P/N 44203, Yellow Springs Instrument Corp.) protected from radiant heat exchange by a shield (Model No. 43103A, R. M. Young Co.) was used to measure air temperature. Wind speed was measured with a cup anemometer (Model No. 6101, R. M. Young Co.). Wind speed was corrected by 0.715 m/sec, which is the velocity necessary to begin cup rotation. An Eppley Black & White pyranometer (Model 8-48, Climatronics Corp.) was used to measure incoming solar radiation. Net radiation was measured with a Fritschen net radiometer (Model 3030, Weathertronics). All sensors were mounted on a specially designed assembly and secured approximately ¾ up the trunk (15.8–22.6 m) on the south side of the selected roost tree. The sensors were leveled after attachment to insure proper response.

Signals from the sensors were conducted through moisture-proof connectors and plastic-jacketed, electrically-shielded, multipair cables. The recorder (Model CR5, Campbell Scientific, Inc.) was placed in a metal box at the base of the roost tree. A small circuit board was added to the recorder to modify the signals so that they were within the proper voltage range for the recorder. The recorder contained a four-channel integrator which took 0.3-sec samples of the signals every 2.4 sec and computed time averages. The millivolt average of each channel was printed on paper tape at 2-h intervals. In addition, the printer identified each set of measurements by date and time (end of 2-h average) of collection. The entire system was powered by a sealed, lead-acid battery to assure reliable operation during periods of low temperature.

Pretesting of the four microclimate recording systems at the same conditions showed excellent agreement among each of the measured variables. Temperature and solar radiation measurements were within ±1%. Windspeed measurements were within ±3% of each other, and net radiation compared to within ±8%. These tests were conducted over a uniform grass surface at a height of 1 m.

We defined night as those hours between 18:30 and 04:30 PST to assure that no daylight (shortwave radiation) would be included in the energy metabolism analysis for any days between Oct. and March. Because the CR5 recorder printed 2-hr means for all variables, night was divided further into five recording periods. To eliminate bias between roosts due to comparing values printed at different times (e.g., 22:45 vs 21:00), data were interpolated to represent the same time periods for each roost.

Collection of microclimate data in the Three Sisters roost was restricted to 27–30 Oct. 1979 and 13 Feb. to 13 March 1980 because of animal damage to the cable. Data from all other roosts were grouped into two periods: "late-winter," corresponding to data collected at Three Sisters, and "midwinter," corresponding to data collected during periods when equipment at Three Sisters was not in operation.

Statistical methodology.—Minimum (2-h) daily temperature and maximum (2-h) daily windspeed of roosts and Kingsley Field were compared to determine whether any of these areas offered protection against weather. To determine whether differences in microclimate between roosts were biologically significant to Bald Eagles, total energy (TE) and peak metabolic production rate (PMP) for each night at each roost were estimated using an energy metabolism model.

Variation in microclimate variables within each roost was much greater than that between roosts due to large scale changes in conditions as a result of time of day and major weather systems moving through the area. In order to remove this large variation in microclimate in each roost so that difference in microclimate between areas could be examined, each area's maximum wind speed, minimum temperature, TE, and PMP were referenced to the average of all roosts for any particular day by subtracting the mean values for all roosts from the values in each roost each day. Multivariate analysis of variance was used to determine significant differences between areas on the basis of climatic variables and energy requirements. The union-intersection method was used to test for differences (Morrison 1976:170–224), because it leads directly to simultaneous confidence intervals for group or response differences.

To determine which factors were important to roost preference by Bald Eagles, multiple regression was performed for each roost with relative (% of total) Bald Eagle population at a particular roost as the dependent variable. Average TE for three nights prior to an eagle census at a particular roost and relative use of each of three feeding areas by Bald Eagles were the independent variables.

DEVELOPMENT OF THE ENERGETICS MODEL

Models of energy metabolism have been developed for mammals (Monteith 1973) and birds (Robinson et al. 1976, Walsberg and King 1980, Hayes and Gessaman 1980). The model used in our study has similar assumptions and definitions, and a more detailed description is presented in Keister (1981). (See Table 1 for definitions of symbols.) Assumptions used to develop the equations were:

(1) The shape of a Bald Eagle may be approximated by that of a cylinder with length 0.508 m and a diameter of 0.190 m with a feather thickness of 0.0254 m (based on measurements of three Bald Eagles).
(2) The Bald Eagle is dry, i.e., heat loss by evaporation due to being wet is negligible.

TABLE 1.
DEFINITIONS OF SYMBOLS USED IN AN ENERGY METABOLISM MODEL FOR A BALD EAGLE

A	Surface area of a bald eagle (m^2)
C_p	Specific heat of air (1010 J/kg°K)
D	Diameter of a bald eagle (m)
d	Density of air (kg/m^3)
e	Thermal emissivity
G_2	Conductive heat loss to the perch (W/m^2)
HE	Evaporative heat loss (W/m^2)
k	Thermal conductivity of air (W/m°K)
M	Metabolic heat production rate (kcal/h)
Nu	Nusselt number
PMP	Peak metabolic production rate for a particular night (kcal/h)
r_b	Resistance to heat loss through skin and feathers (sec/m)
r_h	Resistance to convective heat loss (sec/m)
r_r	Resistance to radiative heat loss (sec/m)
r_{hr}	Resistance to convective and radiative losses, operating together (sec/m)
Re	Reynolds number
Rm	Radiation measured by a net radiometer (W/m^2)
S	Stefan-Boltzmann constant (5.67×10^{-8} $W/m^2°K^4$)
T_a	Ambient temperature (°K)
T_b	Body temperature (°K)
T_e	Effective environmental temperature (°K)
TE	Total metabolic energy required for a Bald Eagle to stay overnight in a particular roost and maintain a constant body temperature (kcal)
v	Kinematic viscosity of air (m^2/sec)
W	Wind speed (m/sec)

(3) The body temperature remains constant at 40°C. (Hayes and Gessaman [1980] and Stalmaster [1981] found body temperatures of large raptors varied only slightly near 40°C.)
(4) The ratio of evaporative heat loss from respiration to total metabolic production (HE/m) is 0.10 (Robinson et al. 1976, Calder and King 1974).
(5) The ratio of conductive heat loss to a perch to total metabolic production (G_2/m) is 0.02. (This term has rarely been measured for animals [Monteith 1973:152]. The term is small but must be >0.0 so 0.02 was assumed for completeness. Its inclusion has negligible effects on the model.)
(6) The resistance of the Bald Eagle feather layer to heat loss (r_b) is the same per unit thickness (70% of still air) as that of a red fox (*Vulpes vulpes*) and resistance of Bald Eagle skin is comparable to other animals (Monteith 1973:122).
(7) Resistance to heat loss (r_b) through feathers per unit feather thickness decreases with increasing windspeed at the same rate as that of a White-crowned Sparrow (*Zonotrichia leucophrys*) (Robinson et al. 1976).
(8) Thermal emissivity of feathers (e) is 0.98 (Hammel 1956).

These assumptions were used to develop the following equations:

(1) Effective environmental temperature (T_e) = $T_a + Rm(r_{hr})/dC_p$.

(2) Metabolic heat production rate (M) = $0.977AdC_p(T_b - T_e)/(r_{hr} + r_b)$ in kcal/hr (the constant 0.977 contains the appropriate conversion factor to change from watts to kcal/hr).

(3) Total energy requirement (TE) = $2\sum_{i=1}^{5} M_i$, i = each 2-hr period during night.

Where, Rm = radiation measured by the net radiometer and can be shown mathematically to be equivalent to the radiation received by an eagle if the plumage surface were at air temperature (isothermal net radiation).

Resistance, (r_{hr}), is computed by $1/r_{hr} = 1/r_r + 1/r_h$ and its components by:

resistance to radiant heat loss (r_r) = $dC_p/4eST_a^3$ and
resistance to convective heat loss (r_h) = dC_pD/kNu.

Convective heat transfer, which determines the magnitude of r_h, depends only on forced convection when the Grashof number is $<0.1Re^2$ (Monteith 1973:103), where Re is the Reynolds number computed as WD/v. Therefore, for a cylinder with a diameter of 0.19 m, forced convection applies when wind speed (W) $\geq$ 0.73 m/s. In these calculations, W is almost always greater than 0.73 m/sec because of the inability of the anemometer to measure wind speeds below 0.715 m/sec (see *Microclimate instrumentation*). The appropriate equations are:

Nusselt number (Nu) = $0.024Re^{0.81}$ if W > 2.8 m/sec or,
(Nu) = $0.17Re^{0.62}$ if W $\leq$ 2.8 m/sec.

And, from regression of tabular values at various temperatures,

density of air (d) = $1.294 - 0.00466(T_a - 273.16)$,
thermal conductivity of air (k) = $2.431 \times 10^{-2} + 6.6 \times 10^{-5}(T_a - 273.16)$, and
kinematic viscosity of air (v) = $1.331 \times 10^{-5} + 8.6 \times 10^{-8}(T_a - 273.16)$.

The resistance to heat loss through skin and feathers (r_b) decreases with increasing wind speed (W) because wind penetrates the feathers, $r_b = 916 - 12.8W^{0.5}$.

The following example, constructed from measured values, illustrates the use of these equations:

If, Rm (net radiation) = -4.44 W/m^2,
T_a (ambient temperature) = 277.32°K, and
W (wind speed) = 0.73 m/sec;

then, $r_b = 916 - 12.8(W)^{0.5} = 916 - 12.8(0.73)^{0.5} = 905.0$ sec/m
$d = 1.2924 - 0.00466(T_a - 273.16) = 1.273$ kg/m^3
$k = 2.431 \times 10^{-2} + 6.6 \times 10^{-5}(T_a - 273.16) = 2.458 \times 10^{-2}$ W/m°K
$v = 1.331 \times 10^{-5} + 8.6 \times 10^{-8}(T_a - 273.16) = 1.367 \times 10^{-5}$ m^2/sec

and, $Re = WD/v = (0.73)(0.19)/(1.367 \times 10^{-5}) = 1.015 \times 10^4$
$Nu = 0.17Re^{0.62} = 51.82$
$r_r = dC_p/4eST_a^3 = 271.2$ sec/m
$r_h = dC_pD/kNu = 191.8$ sec/m
$r_{hr} = 1/(1/r_h + 1/r_h) = 112.3$ sec/m

Therefore, $T_e = T_a + Rm(r_h)/dC_p = 277.32 + (-4.44)(112.3)/(1.273)(1010)$
$= 276.93$°K and,

$$M = 0.977AdC_p(T_b - T_e)/(r_{hr} + r_b)$$
$$= (0.977)(0.303)(1.273)(1010)(313.16 - 276.93)/(112.3 + 905)$$
$$= 13.56 \text{ kcal/h}$$

Then, total energy expended (TE) for a 2-h period is,

$$TE = 2 \times 13.56 = 27.11 \text{ kcal}$$

RESULTS AND DISCUSSION

Microclimate of roosts.—The minimum (2-h) daily temperature varied greatly within each roost. The mean for all roosts ranged from 8.0 to −14.9°C during the winter and fluctuated as much as 15.0°C in a 5-d period (Fig. 1). High variability in temperature for all roosts was predominate over any seasonal changes. Maximum (2-h) daily wind speed was relatively low for the Mt. Dome and Bear Valley roosts with a high of 2.5 m/sec for the two sites (Fig. 2). Maximum daily wind speed was greater and more variable for the Three Sisters and Caldwell roosts than for the other roosts, with a high of 6.9 m/sec. Maximum daily wind speed was greater and more variable for the Kingsley weather station than for any of the roosts, with a high of 17.4 m/sec (Fig. 2).

When weather conditions for midwinter were compared, several differences were found between areas. The minimum temperature at the Kingsley weather station was significantly less ($P \leq 0.05$) than for any roost except Mt. Dome (Table 2). Maximum windspeed also was significantly greater ($P \leq 0.01$) for Kingsley weather station than for any roost. In addition, maximum windspeed at the Caldwell roost was significantly greater ($P \leq 0.01$) than that for Mt. Dome and Bear Valley. During late winter, maximum windspeeds were similar for Caldwell and Three Sisters but significantly greater ($P \leq 0.01$) than those for Mt. Dome and Bear Valley. Maximum windspeed at Kingsley weather station was greater ($P \leq 0.05$) than that of any roost; the minimum temperature of the Kingsley weather station, however, was not less ($P > 0.05$) than the average minimum temperature for all roosts during late winter. Minimum temperature for Mt. Dome was less ($P \leq 0.01$) than the minimum temperature of Kingsley and the other roosts during late winter.

The movement of cold air from high to low elevation may have been prevalent during midwinter but not during late winter, resulting in lower temperatures at Mt. Dome (~610 m higher) than at Kingsley during late winter. The Caldwell and Three Sisters roosts had higher winds than the Mt. Dome and Bear Valley roosts because of the topographical differences between the areas. Mt. Dome and Bear Valley roosts are both on northeast facing slopes that provide protection from major weather systems from

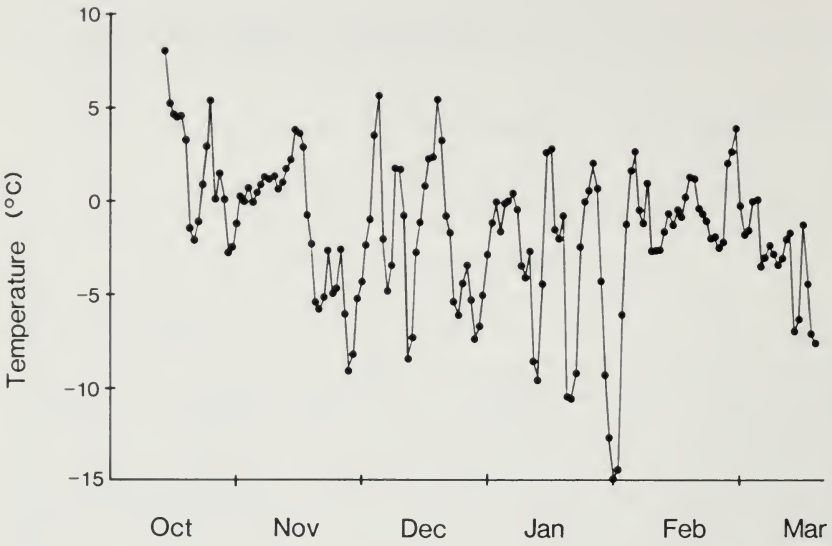

FIG. 1. Mean minimum daily roost temperatures of four Bald Eagle communal roosts in the Klamath Basin, 1979–80.

the south and west. The Three Sisters and Caldwell roosts are not on slopes and therefore were more exposed to prevailing winds. However, both of these roosts lie in slight depressions, and nearby buttes and trees provided some protection from wind. The wind speeds experienced in all roosts were significantly lower than those at the Kingsley weather station, which is located on the floor of the Basin with no protective topography. These data indicate that Bald Eagles in the Klamath Basin selected areas for communal roosting that have more favorable microclimates than the basin floor where feeding areas are located, and that differences in microclimate also exist between communal roosts.

Roosting energy requirements.—The nightly energy demand on Bald Eagles within each roost varied greatly (Fig. 3): from less than 120 kcal in Bear Valley in mid-October to 209 kcal in Mt. Dome in late January. Higher temperatures, lower radiation losses, and lower winds in Bear Valley (Table 2) contributed to a significantly lower ($P \leq 0.01$) metabolic demand than any other roost during both mid- and late winter (Fig. 4). Bear Valley had a 5.6 kcal/night (4% of the mean nightly energy demand) energy savings over the Caldwell roost during midwinter and a 10.5 kcal/night (7%) savings over the Mt. Dome roost in late winter (Table 3). The energy demand in Mt. Dome was significantly greater ($P \leq 0.01$) than in any other roost during late winter (Fig. 4, Table 3) due to a lower tem-

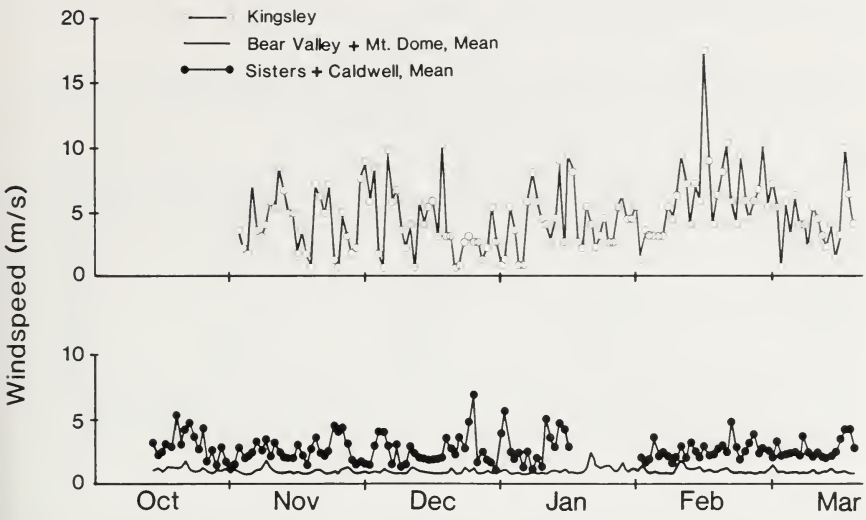

FIG. 2. Maximum daily windspeed recorded for Bald Eagle communal roosts and Kingsley weather station in the Klamath Basin, 1979–80.

perature during that period (Table 2). The energy demands in the Caldwell and Three Sisters roosts were similar to each other but between those of Bear Valley and Mt. Dome during late winter (Fig. 4, Table 3).

We wanted to compare energy demands between the roost with the mildest microclimate (Bear Valley) and feeding areas on the basin floor (represented by Kingsley weather station). Weather instrumentation and collection methods, however, were different between Bear Valley and Kingsley weather station and therefore data were not directly comparable. To compare these areas, we made the conservative assumption that net radiation loss at night was equal for the 2 locations (0.0 W/m^2) and further that T_a = 268.16°K (−5°C), W = 2 m/sec for Bear Valley. Weather differences found between the two areas (Table 2) were then used to estimate conditions at Kingsley (for midwinter T_a = 266.36°K, W = 4.85 m/sec and for late winter T_a = 268.27°K, W = 6.23 m/sec). The metabolic production rate for eagles at Bear Valley under these conditions (18.13 kcal/h) was ~10% lower than that for Kingsley weather station in midwinter (19.87 kcal/h) and ~6% lower in late winter (19.16 kcal/h). Stalmaster (1981) calculated a savings of 7.8–9.8% (depending on radiation loss) in nightly energy production for Bald Eagles roosting in coniferous forests as compared with that in deciduous, riparian areas. Walsberg and King (1980) studied the microclimate of roost and nonroost areas of American

TABLE 2

MEAN DIFFERENCES IN MINIMUM TEMPERATURE AND PEAK WIND SPEED FOR FOUR COMMUNAL ROOSTS AND THE BASIN FLOOR (KINGSLEY) IN THE KLAMATH BASIN DURING THE WINTER OF 1979–80[a]

Area	Minimum temperature (°C)		Peak wind speed (m/sec)	
	Midwinter	Late-winter	Midwinter	Late-winter
Bear Valley	0.35	0.67	−0.52	−0.67[b]
Caldwell	0.06	0.47	1.22[c]	0.90
Three Sisters	—	0.42	—	0.74
Mt. Dome	−0.41	−1.55[c]	−0.71	−0.97[b]
Kingsley	−1.45[c]	0.78	2.33[c]	3.56[c]

[a] Differences were calculated by subtracting the daily (24-h day) mean condition of all roosts from conditions in each area each day (see Statistical Methodology). A value of 0.0 would indicate no difference from the roost average.
[b] Peak windspeed in Bear Valley and Mt. Dome is significantly ($P \leq 0.05$) less than in Caldwell and Three Sisters.
[c] Value is significantly different ($P \leq 0.05$) from the roost average.

Robins in southeastern Washington and found a 4.4% reduction in energy demand within the roost.

Bald Eagles have been observed to shift roosting locations in response to stressful weather (Edwards 1969, Platt 1976, Steenhof et al. 1980). In this study, energy demands for the 3 d prior to counts for communal roosts were not significantly ($P > 0.05$) correlated to the number of eagles

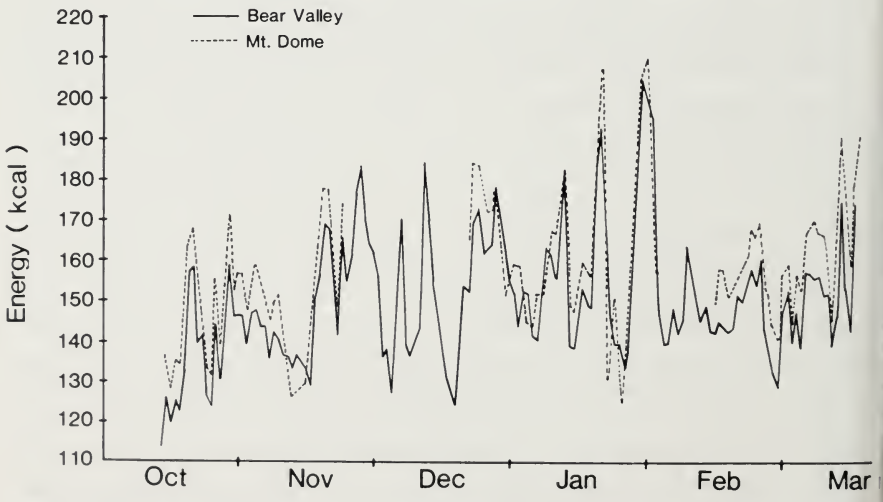

FIG. 3. Nightly energy expended by a Bald Eagle in the Bear Valley and Mt. Dome roosts during winter 1979–80.

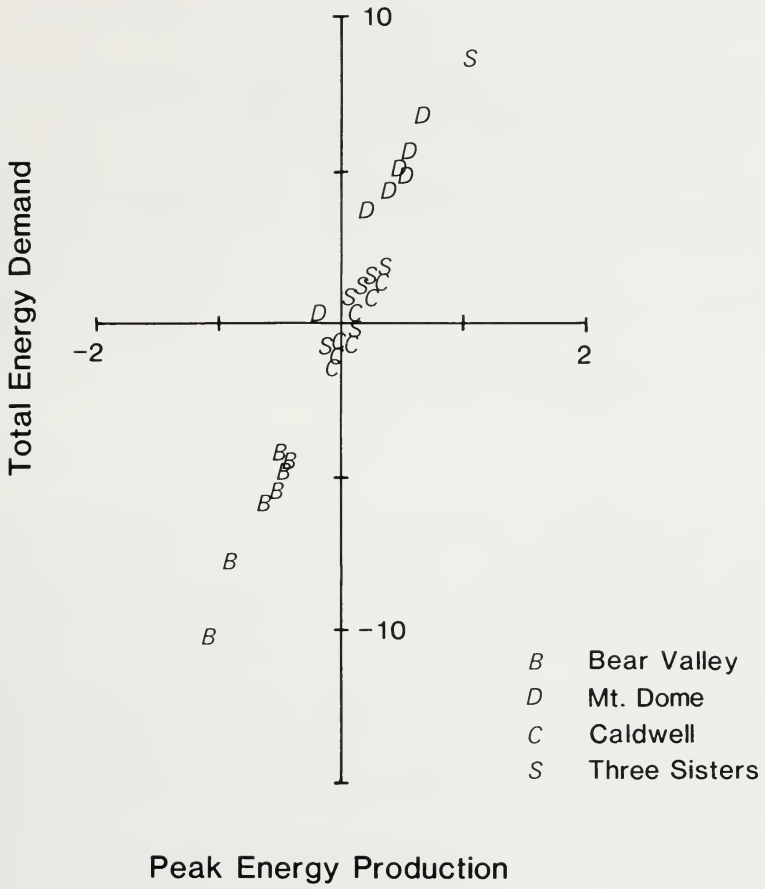

FIG. 4. Differences in total nightly energy demand (kcal) and peak energy production rates (kcal/h) of a Bald Eagle at four communal roosts in the Klamath Basin during late winter 1980. Values were calculated by subtracting the mean condition of all roosts from conditions in each roost each night. The axes represent roost averages.

using the roosts. Instead, numbers of Bald Eagles at a particular roost were positively correlated with eagle numbers at the nearest feeding ground (for four roosts: $r = 0.47$–0.84, $P \leq 0.05$), indicating that Bald Eagles selected roosts closest to where they were feeding. The lack of influence of energy demand on use of different roosts during 1979–80 was possibly due to: (1) high food availability and relatively mild weather conditions resulting in low energy stress, or (2) an increase in energy output required to fly a greater distance to a roost with only a 4–7% increase in nightly energy savings. The first explanation is supported by work done by Hayes

TABLE 3

MEAN DIFFERENCES IN TOTAL NIGHTLY ENERGY DEMAND AND PEAK METABOLIC PRODUCTION OF A BALD EAGLE AT FOUR COMMUNAL ROOSTS IN THE KLAMATH BASIN DURING THE WINTER OF 1979–80[a]

Roost	Total energy (kcal)		Peak metabolic production (kcal/hr)	
	Midwinter	Late-winter	Midwinter	Late-winter
Bear Valley	−3.62[b]	−6.11[b]	−0.386[b]	−0.665[b]
Caldwell	1.99	−0.19	0.305	0.064
Three Sisters	—	1.91	—	0.258
Mt. Dome	1.75	4.39[b]	0.101	0.343

[a] Differences were calculated by subtractng the mean condition of all roosts from conditions in each roost each night. A value of 0.0 would indicate no difference from the roost average.
[b] Value is significantly different ($P \leq 0.05$) than any other roost.

and Gessaman (1980), who found that cold stress began in American Kestrels (*Falco sparverius*) at −5.0°C and 13.47 m/sec wind, but that the most severe conditions used (−17.0°C, 13.47 m/sec, 0.0 W/m^2 radiation) did not appreciably stress Red-tailed Hawks (*Buteo jamaicensis*) or Golden Eagles (*Aquila chrysaetos*). The latter conditions were more severe than weather conditions recorded in this study, and food was observed to be abundant, so Bald Eagles were probably not cold stressed during the 1979–80 winter. The second explanation is supported by Stalmaster and Gessaman (1984), who found that Bald Eagles roosting farther than 3.9 km from feeding areas would incur a net energy loss. If similar assumptions are made for Bald Eagles in the Klamath Basin (flightspeed = 45 km/h, energy for flapping [active] flight = 12.5 × BMR, energy for soaring [passive] flight = 3.5 × BMR, BMR = 12.47 kcal/h; flight to and from roosts in the Klamath Basin is 50% active and 50% passive), the energy cost of flights to and from roosts is 2.22 kcal/km. If a Bald Eagle flew 7 km (14 km round trip) farther to use a more protected roost, the energy cost would be 31.0 kcal. If energy demand were 210 kcal/night (extreme conditions for 1979–80), a 7% energy savings (based on results from this study) would only be 14.7 kcal/night. Therefore, nightly energy savings from selecting a more favorable microclimate would not compensate for the increased energy expenditure required to fly to another roost.

In the Klamath Basin, Bald Eagles fly as far as 20 km (40 km round trip) to roost. This represents an energy expenditure of 88.7 kcal. Energy savings of 10% (the difference between Bear Valley and Kingsley) achieved during severe conditions by staying in a communal roost instead of roosting in the basin would represent 21 kcal/night and would not compensate

for the energy lost in flying to the roost. The shortest distance between any roost and a feeding area is 6 km, with an energy expenditure of 26.6 kcal required for travel. Therefore, communal roosting behavior by Bald Eagles in the Klamath Basin cannot be explained solely on the basis of energy savings. In fact, roosts that are more than about 5 km from the feeding area create an energetic disadvantage to communally roosting Bald Eagles. We conclude that although Bald Eagle roosts had favorable microclimates compared to local weather conditions on the basin floor, energy savings were negated by the cost of flying to these roosts, and the adaptive significance of such behavior must be explained by other phenomena.

SUMMARY

During the winter of 1979–80, microclimatic variables were measured in four Bald Eagle (*Haliaeetus leucocephalus*) communal roosts located in the forests around the Klamath Basin of northern California and southern Oregon. An energetics model for roosting Bald Eagles was developed from microclimatic variables to compare the different roosts. All roosts were relatively protected from high winds in comparison to feeding areas (represented by Kingsley weather station, which was located on the basin floor in nearby Klamath Falls, Oregon) and showed a temperature advantage during midwinter. Higher temperature, lower radiation loss, and lower winds in the Bear Valley roost contributed to a significantly lower ($P \leq 0.01$) nightly energy demand on Bald Eagles than in any other roost. Bear Valley had a 4 and 7% savings in energy demand compared with the most stressful roost, and a 10 and 6% savings compared with Kingsley weather station during midwinter and late winter, respectively. Differential use of the four roosts by Bald Eagles for communal roosting was not related to differences in energy demand between the roosts. Savings in energy due to use of communal roosts during night were not great enough to explain flight of Bald Eagles to roosts in the Klamath Basin.

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CAUSES OF RECORDING ERRORS IN SINGING BIRD SURVEYS

JONATHAN BART

It is well known that in singing bird surveys, even the best surveyors seldom record all of the audible birds (Robbins and Stallcup 1981). This is especially true when there is a pronounced "dawn chorus" because so many birds are vocal then (Bystrak 1981). Experimental evidence has demonstrated that even later in the day, 35% of the audible birds may be missed by experienced field workers (Bart and Schoultz 1984). The experiments yielding this result included a series of simulations in which bird songs were broadcast from loudspeakers surrounding the surveyors. The primary purpose of the simulations was to determine how the proportion of birds recorded varies with the number of birds present. Here, the same data set was used to determine what kinds of recording errors were most common.

There has been little study of the kinds of recording errors made by surveyors in singing bird surveys. Variation in hearing ability, and its effect on survey results, has been studied by Cyr (1981), Faanes and Bystrak (1981), and Ramsey and Scott (1981). Robbins and Stallcup (1981) commented on the difficulty of separating some confusing pairs of species, and Kepler and Scott (1981) reported on a training program designed to reduce the incidence of recording errors. None of these studies, however, provided estimates of the frequency of various kinds of recording errors.

In this study three kinds of error were distinguished—over-counting, under-counting, and mis-identification—and their magnitudes among experienced surveyors were estimated for each of eight species of birds. Various hypotheses were then investigated that explain the source of the errors. The purpose of the study was to help field workers increase the accuracy of singing bird surveys.

METHODS

Twenty-seven loudspeakers were used to broadcast bird songs for a series of 3-min periods during which 20 experienced bird surveyors recorded all species and individuals that they heard. The surveyors all had participated in Breeding Bird Surveys (Bystrak 1981) and were familiar with the songs of all of the species. At the time of the trials they had been birding for an average of 18 years (range = 5–33 years).

The 3-min periods during which we broadcast songs were designed to simulate conditions occurring between 07:00 and 10:00 in June in many parts of eastern United States and Canada. The numbers of species, individuals of each species, durations of song, and song

volumes were controlled, though some of these factors were allowed to vary, as they do on real surveys. We studied the ability of the surveyors to detect 16 species. Nine of the 16 species occurred at densities of one to four per listening period; seven of them occurred at densities of one or two per listening period.

During each listening period, 20 individual birds of 12 or 13 species sang at least once. A total of 39 species occurred during 54 3-min listening periods. Results from 43 periods were analyzed for this report. The others were training periods or periods in which surveyors recorded species but did not attempt to count individuals of each species. For additional details of the simulations, see Bart and Schoultz (1984).

All analyses in this report are based on eight of the nine species that occurred at densities of one to four: Mourning Dove (*Zenaida macroura*), American Crow (*Corvus brachyrhynchos*), American Robin (*Turdus migratorius*), Red-eyed Vireo (*Vireo olivaceus*), Common Yellowthroat (*Geothlypis trichas*), Indigo Bunting (*Passerina cyanea*), Field Sparrow (*Spizella pusilla*), and Song Sparrow (*Melospiza melodia*). Each of these species occurred during 27 of the 43 listening periods. Eastern Wood-Pewees (*Contopus virens*) were eliminated in this analysis because one of the tape recordings included a pewee song that closely resembled a Red-eyed Vireo.

Three types of recording errors were examined: under-counting, over-counting, and mis-identification. Under-counting meant missing some individuals of a species. The under-counting rate was defined as (number of birds missed)/(number present). Over-counting meant recording more individuals of a species than were present when at least one individual of the species was present. The over-counting rate was defined as (number of extra birds recorded)/(number of periods in which the species was present). Mis-identification meant recording one or more individuals of a species that was not present. The mis-identification rate was defined as (number of mis-identifications)/(number of periods in which the species was not present).

For each type of error, an 8 (species) by 20 (observers) matrix was constructed, each cell containing the error rate for one observer and species. Standard errors (SE) for the numbers in each cell were calculated in the following way. Rates of over- and under-counting were strongly related to the number of birds present on the tapes. Consequently, the 27 listening periods with the species present were considered to be a stratified random sample. The 10 periods with one individual present comprised one stratum, the eight periods with two present comprised a second stratum, etc. The periods with the same number of individuals present resemble a systematic sample rather than a random sample as they were designed to exhibit the full range of possible volumes and durations, and, as a result, the variance estimates probably had positive bias. This caused the conclusions to be conservative. The standard errors of mis-identification rates were based on the 16 periods in which the species was absent. These were considered to be a simple random sample. Standard errors of the mean number of each type of recording error for each observer (averaged over all species) and of the mean number of recording errors for each species (averaged over all observers) were calculated using the standard errors from each cell.

Most coefficients of variation (CV) were less than 0.10, indicating that sampling error could safely be ignored in estimating the mean error rates per surveyor or species. The sole exception was that the CV's of the mean mis-identification rates per species averaged about 30% and in a few cases were as high as 70%.

Using the three matrices, I calculated the average rate for each type of error, the range in the error rate among observers, and I attempted to identify factors that influenced the error rates, such as number of individuals of the species present. I then evaluated the null hypothesis that each of the three errors could be attributed solely to the species' average error rate and the surveyor's average error rate plus a random component. Under this model, the predicted error rate for each observer and species is,

$$e_{ij} = \frac{e_{i.} e_{.j}}{e_{..}} \quad (1)$$

where

e_{ij} = predicted error rate for observer i and species j
$e_{i.}$ = average error rate for observer i for all species
$e_{.j}$ = average error rate for species j for all observers
$e_{..}$ = average error rate for all species and observers.

The alternate hypothesis in this test was that observers "discriminate" among species, tending to make more errors than expected for some species and fewer for others. Such discrimination might have occurred for several reasons. For example, a particular surveyor might have been especially familiar with one species due to having studied it intensively. Other causes of discrimination are discussed below. I tested the null hypothesis by counting the number of cells in each matrix in which the deviation between predicted and observed error rates exceeded 2.8 times the standard error of the observed rate. This corresponded approximately to the 0.01 level of significance. There were $20 \times 8 = 160$ cells, and under the null hypothesis the expected number of cells having deviations significant at the 1% level was 1.6.

RESULTS AND DISCUSSION

The average number of birds missed per period (with 20 actually present) was 6.0 (range among surveyors = 4.2–10.8). The average number over-counted was 1.0 (range = 0.2–4.1). The average number mis-identified was 0.6 (range = 0.16–2.1). Among all cases in which birds were "made up" (due either to over-counting or mis-identification) the proportion due to over-counting varied among surveyors from 0.15 to 0.78. Thus some surveyors tended to over-count birds more frequently than they mis-identified them, while for other surveyors the reverse was true.

The number of over-counted birds dropped sharply as the number present increased. The average number over-counted per listening period for all species and observers was 0.24, 0.11, 0.05, and 0.01 as the number of birds present varied from one to four. Thus 24% of the time that one individual of a species was present, observers recorded two or (rarely) more, but when three individuals were present, four or more were recorded only during 5% of the periods.

Many of the mis-identifications could be traced to particular species. One surveyor recorded 21 Vesper Sparrows (*Pooecetes gramineus*) and was clearly mis-identifying Song Sparrows. Another recorded 12 Yellow-breasted Chats (*Icteria virens*), apparently mis-identifying Gray Catbirds (*Dumetella carolinensis*). Both of the surveyors frequently recorded Vesper Sparrows and catbirds correctly. In other cases of mis-identification, it was unclear which species was actually heard. Species with seemingly distinctive songs such as crows and Grasshopper Sparrows (*Ammodramus savannarum*) were mis-recorded fairly often. Mis-identifications thus

probably are not caused solely by confusion between species with similar songs.

A few errors recorded as under-counting undoubtedly were actually caused by mis-identification. Thus, if one Song Sparrow was present, and was heard, but was recorded as a Vesper Sparrow, then I would have recorded the Song Sparrow as having been under-counted. If most incidents of under-counting were caused by mis-identification, however, rather than by failing to record the bird at all, then the mis-identification rate would have been approximately equal to the under-counting rate. The two rates actually differed by an order of magnitude, indicating that under-counting generally was caused by failure to record the species rather than by mis-identifying it.

The simple model (equation 1) that the rates of recording errors are determined by the observer's overall ability and the species' overall difficulty was rejected for over-counting and missing birds, but not for mis-identifications (Table 1). Thus, for example, seven surveyors under-counted Mourning Doves at rates that were significantly higher or lower than expected on the basis of the average under-counting rate for the species and surveyor. Mourning Doves were sometimes mis-identified, but none of the surveyors mis-identified this species significantly more or less often than predicted by equation 1. Two surveyors over-counted Mourning Doves at rates significantly different than predicted by equation 1.

All species were discriminated for or against by some observers, and there were only minor differences between species. The surveyors were slightly more consistent with robins and doves than with the other species, but the difference could easily have been caused by sampling error alone.

Observers varied in the degree to which they showed discrimination. All observers discriminated for or against at least one species. Two surveyors showed discrimination in the numbers missed or over-counted with each of the eight species. The general conclusion of this analysis is that over- and under-counting, and mis-identifications for some surveyors, cannot be attributed solely to the surveyor's overall skill and the species' overall difficulty.

Causes of recording errors.—Two explanations for the failure of the null hypothesis were evaluated. Under the "species specialist" hypothesis surveyors are assumed to be more capable of identifying some species than others. They miss fewer, over-count fewer, and mis-identify fewer of the species that they specialize on. Conversely, under the "favoritism" hypothesis, surveyors preferentially record certain species. When they are uncertain about which species is singing or about whether the individual has already been recorded, they are more likely to record certain species than others.

TABLE 1

NUMBER OF SURVEYORS OUT OF 20 WITH SIGNIFICANTLY HIGH OR LOW RATES OF THREE TYPES OF RECORDING ERRORS MADE DURING A SIMULATION OF BIRD SURVEYS[a]

Species	Type of error		
	Under-counting	Mis-identification	Over-counting
Mourning Dove	7	0	2
American Crow	12	0	6
American Robin	6	0	4
Red-eyed Vireo	9	0	7
Common Yellowthroat	10	0	6
Indigo Bunting	8	0	8
Field Sparrow	9	0	7
Song Sparrow	8	0	5

[a] $P < 0.01$ using a t-test.

These explanations are not mutually exclusive, but they do lead to different, and testable, predictions. Under the species specialist hypothesis, if a surveyor is especially capable of identifying a particular species, then the frequencies with which he misses, over-counts, or mis-identifies the species should all be lower than predicted by equation 1, and thus the deviations, observed rate–expected rate, should all be negative. If he is especially poor at identifying the species, then each of the deviations should be positive. Thus, under this hypothesis, all three deviations for each surveyor should have the same sign (apart from sampling error). Consequently, if we select a single species, and construct a bivariate plot of any two of the deviations using the data from all surveyors, then we should find a positive relationship.

The situation is different under the hypothesis that surveyors show favoritism. If a surveyor shows favoritism towards a species—meaning that in the presence of uncertainty he tends to record the favored species—then the frequencies with which he over-counts and mis-identifies the species are greater than predicted by equation 1. The surveyor misses the species less often than predicted, however, because he records it when he would hesitate to write down other species. Thus the deviations for over-counting and mis-identification are positive while the deviation for under-counting is negative. If the surveyor avoids recording the species when uncertain, then the deviations for over-counting and mis-identification are negative while the deviation for under-counting is positive. Under the favoritism hypothesis, if we select one species and prepare a bivariate plot of the over-counting and mis-identification deviations we expect to find a positive relationship. If we compare over-counting and under-

TABLE 2

CORRELATION COEFFICIENTS AMONG THREE TYPES OF RECORDING ERRORS MADE BY 20 SURVEYORS IN A TAPE-RECORDED SIMULATION OF EARLY MORNING BIRDSONGS

Species	Errors		
	Over-counting vs mis-identification	Under-counting vs mis-identification	Under-counting vs over-counting
Mourning Dove	0.337	−0.717	−0.378
American Crow	0.481	−0.163	−0.662
American Robin	0.287	−0.309	−0.553
Red-eyed Vireo	0.108	−0.170	−0.580
Common Yellowthroat	0.167	−0.080	−0.547
Indigo Bunting	0.123	−0.383	−0.362
Field Sparrow	0.244	−0.179	−0.414
Song Sparrow	0.100	−0.263	−0.509

counting or mis-identification and under-counting, we expect the correlation to be negative.

Both hypotheses thus predict a positive correlatiion between deviations from the expected rates of over-counting and mis-identification, but the other two correlations (under-counting vs over-counting and over-counting vs mis-identification) are predicted to be positive under the specialist hypothesis and negative under the favoritism hypothesis.

To distinguish between these hypotheses, correlation coefficients were calculated for each pair of deviations from the error rates expected using equation 1. Each species was analyzed separately so each coefficient was based on 20 pairs of observations, one pair for each surveyor. A bivariate plot of each data set was inspected, and the coefficients were calculated both with and without possible outliers. Omitting possible outliers did not change any of the coefficients significantly so all of the data were used in all cases. None of the plots had detectable non-linear trends.

Rates of over-counting and mis-identification were positively correlated for all species as predicted by both the specialist and favoritism hypotheses (Table 2). The deviations between numbers missed and over-counted were negatively correlated in all eight species as were the numbers missed and mis-identified. Both of these trends are predicted by the favoritism hypothesis, but not by the species specialist hypothesis. It thus appears that the variability in recording errors, not explained by the observer's ability and the species' difficulty, is largely due to personal biases for or against particular species. Such biases lead the observer to assign preferentially uncertain cues to certain species rather than to others. The practical im-

TABLE 3

RATIO OF NUMBER OF INDIVIDUAL BIRDS RECORDED TO NUMBER ACTUALLY PRESENT FOR 20 SURVEYORS AND 8 SPECIES OBTAINED FROM A TAPE-RECORDED SIMULATION

	Species[a]								
Surveyor	MODO	AMCR	AMRO	REVI	COYE	INBU	FISP	SOSP	Mean
1	0.61	0.63	0.61	0.61	0.72	0.65	0.70	0.60	0.64
2	0.97	1.33	0.88	0.90	1.05	1.21	1.23	0.65	1.03
3	0.77	0.56	0.65	0.65	0.86	0.72	0.70	0.81	0.71
4	0.75	0.91	0.88	1.07	0.91	1.12	1.18	0.88	0.96
5	0.51	0.75	0.72	0.83	0.86	0.84	0.83	0.65	0.75
6	0.84	1.02	0.75	0.77	0.61	0.72	0.79	0.42	0.74
7	0.49	0.70	0.32	0.53	0.65	0.61	0.74	0.47	0.56
8	0.67	0.97	0.86	0.67	0.70	0.75	0.79	0.54	0.74
9	0.88	0.88	0.51	0.42	0.47	0.47	0.61	0.44	0.59
10	0.68	0.60	0.79	0.75	0.74	0.90	0.79	0.61	0.73
11	0.72	0.75	0.77	1.00	1.09	0.90	0.95	0.97	0.89
12	0.77	0.81	0.75	0.79	0.77	0.79	0.75	0.77	0.78
13	0.61	0.84	0.56	0.77	0.23	0.44	0.90	0.35	0.59
14	0.74	0.81	0.68	0.81	0.79	0.79	0.72	0.58	0.74
15	0.77	0.67	0.75	0.83	1.07	0.84	0.95	0.79	0.83
16	0.70	0.74	0.75	0.70	0.77	0.91	0.77	0.70	0.76
17	0.63	0.67	0.58	0.65	0.49	0.39	0.53	0.56	0.56
18	0.61	0.74	0.75	0.79	0.84	0.93	0.72	0.61	0.75
19	0.90	1.05	0.14	0.49	0.70	0.53	0.88	0.54	0.65
20	0.74	0.83	0.70	0.90	0.61	0.72	0.68	0.58	0.72
Mean	0.72	0.81	0.67	0.75	0.75	0.76	0.81	0.63	0.74

[a] MODO = Mourning Dove; AMCR = American Crow; AMRO = American Robin; REVI = Red-eyed Vireo; COYE = Common Yellowthroat; INBU = Indigo Bunting; FISP = Field Sparrow; SOSP = Song Sparrow.

portance of this result is that surveyors may be able to discern the species they show favoritism towards and adjust their recording practices.

Window species.—Kepler and Scott (1981) reported that in training sessions inexperienced surveyors often missed one or two species at unexpectedly high rates. They referred to these as "window species", the name being derived from the tendency of the surveyor to listen "through" the song, even when it was quite audible. Although the surveyors in the present study were far more experienced than the participants in Kepler and Scott's training sessions, it seemed worthwhile to determine whether there was any evidence of window species in the simulation. For this discussion, the term efficiency is defined as the total number of a species recorded divided by the total number present on the tapes.

The efficiencies for each surveyor and species were calculated and inspected for markedly low values (Table 3). The results showed that there

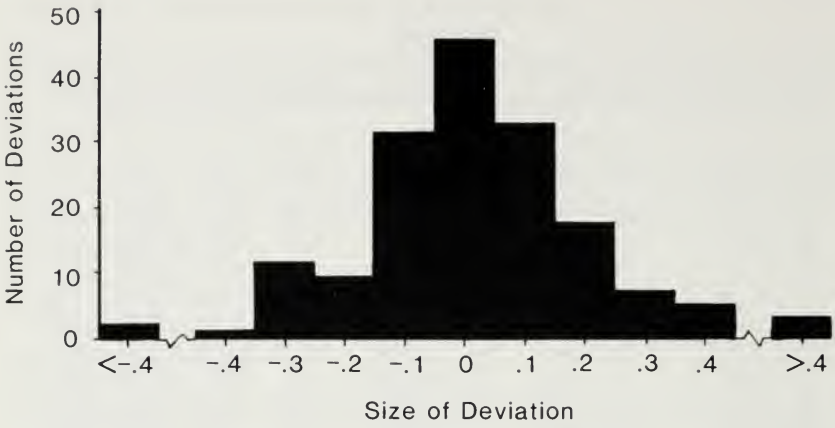

FIG. 1. Frequency distribution of deviations between expected and actual efficiencies for 20 surveyors recording eight species of birds. Expected values calculated using equation 1 (see text). Deviations are expressed as (observed − expected)/expected.

was no strong tendency for this to occur. There are some low values, but markedly high efficiencies—some exceeding 1.0, indicating that, on average, more birds were recorded than were present—were also common.

The occurrence of window species should cause negative skewness in the efficiencies because of the prevalence of very low values. To investigate this possibility, the predicted efficiency for each surveyor and species was calculated using equation 1 with efficiencies rather than error rates. The proportional deviation from the predicted efficiency was then calculated as (observed efficiency − predicted efficiency)/observed efficiency. If window species were important to the surveyors in this study, then the frequency distribution of these proportional deviations should show marked negative skewness. The distribution, however, is almost perfectly symmetric (Fig. 1). Thus, our surveyors had few if any pronounced window species, or if they did tend to listen through some species' songs, such tendencies were only one aspect of a constellation of errors including over-counting and mis-identification as well as under-counting. It should be noted, however, that all of our surveyors had extensive experience with all the species analyzed in this study. If the surveyors had been tested on species with which they were less familiar it is quite possible that window species would have been more evident.

Simultaneous recording.—Surveyors sometimes record together, but independently, to estimate what fraction of the birds present each surveyor has recorded. Two tacit assumptions of this method are that at least one surveyor records every audible bird and that neither surveyor records

birds that are not present. The results of this study suggest that both of these assumptions are probably inaccurate to a significant degree, and this makes estimating surveyor accuracy more complex. Most surveyors presumably would like to know both what proportion of the birds they identify correctly, and how often they record birds not actually present. This section presents both theoretical and empirical evidence that simultaneous recording by two surveyors does not produce a highly accurate estimate of the proportion of birds correctly detected. In this discussion no distinction is made between birds that are over-counted and those that are mis-identified. I will refer to both as birds that are "made up."

To consider how well the proportion of birds correctly identified by a surveyor called "one" is estimated, let the correct identification rate = a/b and the estimate of this rate = $(a + c)/(b + d - e)$, where a = number correctly identified by surveyor one; b = total number present; c = number made up by surveyor one; d = number made up by both surveyors; and e = number missed by both surveyors.

The numerator of the estimated rate cannot be smaller than the numerator of the actual rate. If d is smaller than e, then the denominator of the estimate is smaller than the denominator of the actual rate. Thus, if the number of birds mis-identified and over-counted by both surveyors is less than the number missed by both surveyors, then the estimate will be greater than the actual rate. As most surveyors made up only one or two birds per listening period and missed at least four birds per period, it can be predicted that the correct identification rate is usually overestimated when surveyors record in pairs.

This prediction was tested by forming 21 random pairs of surveyors and analyzing the data they obtained in the 43 listening periods. I tallied the number of birds correctly detected, made up, and missed by each observer, and I calculated the actual and estimated correct identification rates for each member of each pair using the formulas above. All but one of the 42 estimates exceeded the actual rate. The average ratio of the estimated rate to the actual rate for all 42 estimates was 1.17 (range = 0.85–1.43). These results pertain to all species combined. The results for species considered separately were similar. The average ratio was also 1.17 (range = 1.06–1.34).

Estimates of a surveyor's correct identification rate varied by up to 0.10 depending on who the second surveyor was. For example, the average of seven estimates for one surveyor was 0.80, (range = 0.79–0.86). The actual proportion correctly detected was 0.69. Thus simultaneous recording by two surveyors should not be viewed as an accurate method of estimating the correct identification rate.

Surveyors are also likely to be interested in estimating how frequently

they over-count or mis-identify birds. There does not appear to be any simple analytical way of estimating how many birds are made up when surveyors record in pairs. The most practical remedy is probably to compare records immediately after each listening period and then spend a minute or two attempting to resolve discrepancies. My experience with this practice is that many of the mis-identification and over-counting errors can be identified. The method is less effective in identifying birds missed by both surveyors because when a bird is first heard after the listening period, there is usually no way to determine whether it sang during the listening period.

If some of the birds over-counted or mis-identified can be detected by spending an additional minute or two after the recording interval, then the question arises: should these errors be eliminated in calculating the estimate of the proportion correctly recorded by each surveyor? For example, suppose one surveyor records 10 birds, and the number recorded by both surveyors is 15, but subsequently three of these are discovered to be over-counting errors, all made by the second surveyor. Then should the proportion correctly identified by surveyor one be estimated as 10/15 or 10/12? It might seem that the latter estimate is preferable, but this is not necessarily true because some birds are missed by both surveyors. In fact, as shown below, the former estimate may well be more accurate.

If all the birds made up are eliminated, then the estimate of the correct identification rate presented above becomes $a/(b - e)$. By rearranging the equations, it can be shown that this will be greater than the estimate using all of the records $(a + c/b + d - e)$ if

$$\frac{\text{no. made up by surveyor one}}{\text{no. made up by both surveyors}} < \frac{\text{no. correctly recorded by surveyor one}}{\text{no. correctly recorded by both surveyors}}$$

The term on the left is usually between 0.40 and 0.60 because most surveyors make up about the same number of birds but seldom make the same errors. The term on the right is usually at least 0.8 because most of the birds recorded correctly by one surveyor are also recorded correctly by the other surveyor. Thus the inequality usually holds, and it can therefore be predicted that removing all of the made-up birds will usually increase the estimate of the correct identification rate.

This prediction was tested by further evaluation of the 21 random pairs of surveyors. In the analysis above, the correct identification rate was estimated for each member of each pair using all of the records. The made-up birds were then removed and the estimates were recalculated.

As predicted, removing the made-up birds increased all but two of the 42 estimates. When made-up birds were included, the estimated correct identification rate was, on average, 17% too high. When the made-up birds were eliminated, the rate averaged 24% too high.

Thus, even if one can identify birds that were over-counted or mis-identified, it appears best to use the original counts in estimating the proportion detected correctly. This somewhat paradoxical result indicates simply that paired observations are not a very accurate way of estimating the correct identification rate. Simultaneous observations, however, are an excellent means of uncovering and correcting various other recording errors, especially if the surveyors compare results immediately after each listening period. Furthermore, these cautions apply mainly to the common custom of recording all detectable individuals of all species. If only certain species are recorded or distant songs are excluded, then simultaneous recording can certainly be made to yield accurate estimates of the various recording errors.

SUMMARY

Data from a tape recorder simulation reproducing what is heard on singing bird surveys in June in the northeastern United States were used to estimate the frequency of three types of recording errors. On average, 20 experienced surveyors missed about 30% of 20 birds present on the recordings and made up an average of 1.8 birds/3-min listening period. About one-third of the birds made up were due to mis-identifications; the rest were due to over-counting (e.g., recording three birds when only two were present).

An investigation of the variation in recording errors among surveyors indicated that they tended to discriminate among species, recording some at higher or lower rates than expected on the basis of the species' difficulty and the surveyor's ability. This tendency was referred to as discrimination because the number of individuals recorded was affected by factors other than the species' difficulty and the surveyor's overall ability. Both negative discrimination (recording fewer individuals than expected) and positive discrimination (recording more individuals than expected) were common.

Two hypotheses were investigated to explain discrimination: that the surveyors are species specialists having particularly high ability with some species; and that surveyors show favoritism, tending to record certain species preferentially when there is uncertainty about the true identity of a bird. Analysis of the tape recorder data clearly supported the favoritism hypothesis. The concept of window species, which has been shown in other studies to apply to inexperienced surveyors, had little explanatory power in this study, which used experienced surveyors.

The process in which two surveyors record together, but independently determine which fraction of the birds present each is detecting, over-estimates the proportion of birds correctly identified. Simultaneous recording is effective, however, in revealing birds that were made up, especially if surveyors compare their records immediately after each listening period.

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STUDENT MEMBERSHIP AWARDS FOR 1985

Student Membership Awards in the Wilson Ornithological Society have been made available from the general funds of the society to recognize students who have the potential to make significant contributions to ornithology. The following students have been selected by the Student Membership Committee for awards this year: Jean V. Adams, Bradley Univ.; Terry Armstrong, Queen's Univ.–Ontario; James F. Bergan, Texas Tech. Univ.; Reed Bowman, MacDonald College; Michael W. Brown, Iowa State Univ.; David G. Cook, Texas Tech. Univ.; Thomas I. Crossman, Univ. Connecticut; Clyde D. Cummins, Miami Univ.; Tristan J. G. Davis, Louisiana State Univ.; Barrett A. Garrison, Virginia Polytechnic Institute and State Univ.; Joseph A Gubanyi, Univ. Nebraska; Danny J. Ingold, Mississippi State Univ.; Walter N. Johnson, Univ. Maine; Nedra K. Klein, Louisiana State Univ.; Natasha C. Kline, Univ. Miami; Jacqueline J. Lape, North Carolina State Univ.; David Lemon, Univ. Toledo; Mei-yao C. Louis, Univ. Minnesota–Duluth; Richard W. Lundquist, Univ. Washington; Sarah J. Madsen, Univ. Washington; D. James Mountjoy, Queen's Univ.–Ontario; David C. Morimoto, Boston Univ.; Cecilia M. Riley, Univ. Arkansas; BethAnn Sabo, George Mason Univ.; Virginia M. Scarpino, State Univ. New York–Geneseo; John M. Shipley, Jr., Idaho State Univ.; Douglas G. Sheeley, Texas Tech. Univ.; Stefen Sobkowiak, MacDonald College–Quebec; Kimberley A. With, San Francisco State Univ. Student Membership Committee, Wilson Ornithological Society—Thomas C. Grubb, Charles F. Leck, Roland R. Roth, Richard N. Conner (chair).

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PATTERNS OF ASSOCIATION OF SECONDARY SPECIES IN ROOSTS OF EUROPEAN STARLINGS AND COMMON GRACKLES

Donald F. Caccamise and Joseph Fischl

Composition of roosting flocks varies from single-species groups to aggregations of many different species. Mixed flocks are often composed of one to three primary species making up the largest proportion of the association, with a variable number of secondary species making up the remainder (Gadgil 1972). Questions relating to the functional significance of communal roosting behavior have been a major focus of recent research (e.g., de Groot 1980, Loman and Tamm 1980, White 1980, Fleming 1981, Weatherhead 1983). However, the role of secondary species in these flocks has received little attention.

Roost studies have generally emphasized primary species, often with observations of secondary species reported only incidentally. Many of the resulting data are incomplete and few are quantified. Also, most studies have emphasized individual roosts and generally have not lasted throughout roosting seasons. For example, Meanley (1965, 1971) did extensive work in the southern U.S. on the biology of blackbird roosts, but provided little information on secondary species. Similarly, Robertson et al. (1978) provided some quantitative information, but most data on secondary species were collected in a single day during 3 man-hours of walks near a large winter roost. Gadgil (1972) discussed the role of mixed roosts, but provided no quantified observations (Gadgil and Ali 1976).

In addressing the question of why mixed-species roosting flocks form, Ward and Zahavi (1973:524) said, "We have not personally found any situations where two or more species with completely dissimilar foods or feeding places form mixed roosts—except where this can be explained in terms of a shortage of suitable roost sites." They later summarized the situations where mixed species roosts may be formed: (a) limited availability of roost sites; (b) where one species selects the communal roost of another species as a safe site (predator protection) for its own communal roost; (c) species with similar foraging requirements roost together in order to share information. Situations (a) and (b) are exceptions to what was otherwise offered as a general explanation for roosting behavior (situation [c]—the information exchange hypothesis).

We believe the apparent conformity of mixed flocks to these situations is largely due to the scant data on secondary species. In this study our main goal was to examine Ward and Zahavi's (1973) prediction that mixed

species roosting flocks generally (allowing for exceptions [a] and [b] above) contain only species with similar feeding requirements. We hypothesized that (1) some secondary species would show consistent patterns of association in many roosts and over long periods while being sufficiently distinct in their foraging requirements so as to preclude benefits from information exchange; and (2) population sizes of some secondary species would be large enough (Pulliam 1973) to provide maximum levels of predator protection without need to further increase flock size by roosting with other species. We did not consider limited availability of roost sites, because earlier studies suggested that this was unlikely in our study area (Lyon and Caccamise 1981, Caccamise et al. 1983). Support for our hypotheses would suggest that information exchange (Ward and Zahavi 1973) alone does not explain aggregation of mixed species into roosting flocks, and that alternative or additional factors are important in their formation.

We examined patterns of association for secondary species in roosts where primary species were European Starlings (*Sturnus vulgaris*) and Common Grackles (*Quiscalus quiscula*). Our approach was to (1) identify secondary species present in all roosting flocks over a large study area; (2) determine seasonal pattern of association for each species within the regional roosting population; and (3) examine the distribution of secondary species among individual roosting flocks on a regional basis.

STUDY SITE AND METHODS

Data collection for secondary species took place during local roosting seasons (June–Nov.) of 1979 and 1980; however, studies of primary species extended from 1977–82 (Caccamise et al. 1983). A region within the piedmont and inner-coastal plain provinces of central New Jersey (Robichaud and Buell 1973) was searched rigorously for all roosts containing at least 2000 birds. Roosting assemblages were located throughout the roosting season by regularly traveling surveillance routes in the evening. Flight lines were identified and followed to roost sites.

The census area included approximately 1000 km^2 (Caccamise et al. 1983). Size was defined initially (1977) by the limits of our ability to conduct thorough censuses. Once the distribution of roosts was determined, we confined our searching to within the perimeter established by peripheral roost sites. To count birds, one to four observers were stationed at roosts where major flight lines could be viewed during evening arrivals or morning departures. Birds were counted by species in 5-min intervals. Counts taken during inclement weather were not included in estimates of population sizes, as roosting activity was erratic at these times. Total population sizes over the census area were based on 100 counts in 1979 and 113 in 1980. Population sizes were estimated at 5-day intervals by summing number of individuals of each species present in each active roost.

RESULTS

There were 24 active roosts within the census area in 1979 and 18 in 1980. Individual roosts were active from 3 to 20 weeks and ranged in

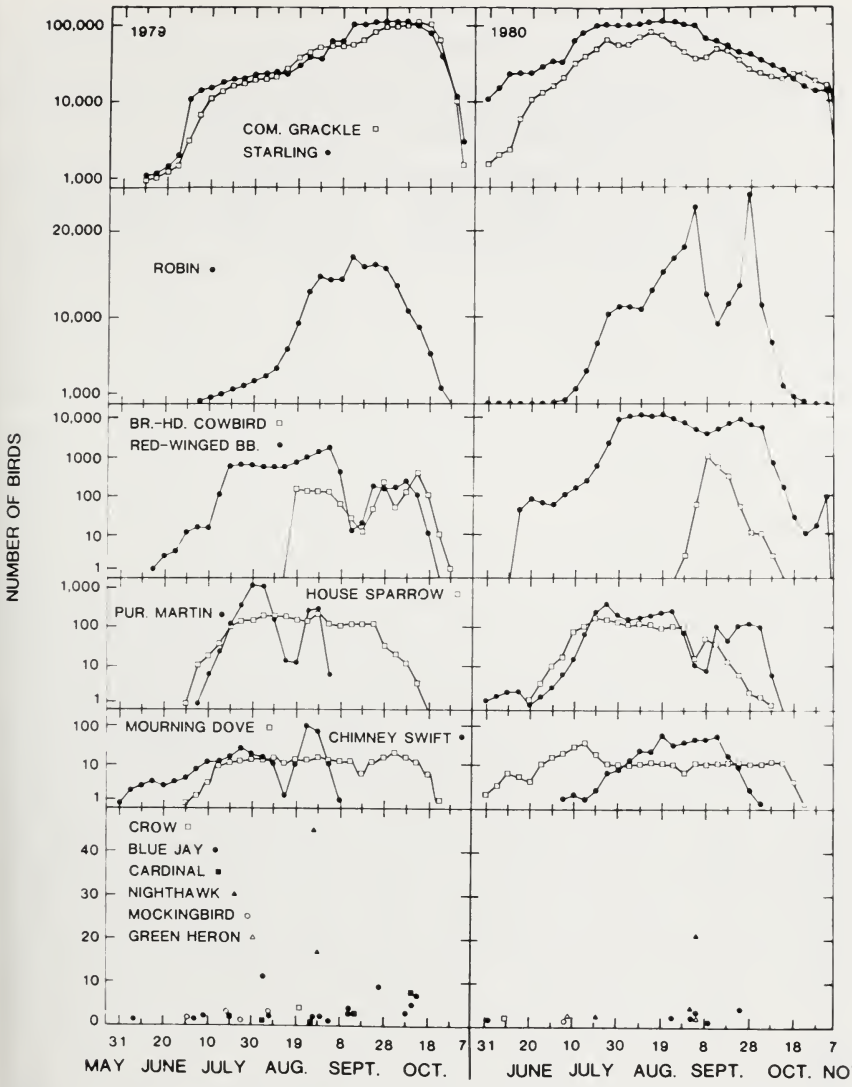

FIG. 1. Number of birds by species in all active roosts in the study area (abbreviations: starling—European Starling; com. grackle—Common Grackle; robin—American Robin; br.-hd. cowbird—Brown-headed Cowbird; red-winged bb.—Red-winged Blackbird; pur. martin—Purple Martin; cardinal—Northern Cardinal; nighthawk—Common Nighthawk; mockingbird—Northern Mockingbird; green heron—Green-backed Heron).

TABLE 1

NUMBER OF ROOSTS WHERE EACH SPECIES WAS RECORDED DURING THE 1979 AND 1980 SEASONS. TOTAL NUMBER OF ROOSTS ACTIVE AT EACH DATE IS EQUAL TO THE NUMBER RECORDED UNDER STARLINGS AND COMMON GRACKLES

	Number of roosts occupied by roosting species[a]															
	Star. grack.		Robin		Br.-h. cowbrd.		Red-wng. blkbd.		Pur. mart.		House sprw.		Chimney swift		Mourn. dove	
Date	'79	'80	'79	'80	'79	'80	'79	'80	'79	'80	'79	'80	'79	'80	'79	'80
10 June	1	3								1			2			2
15 June	1	5					1	1		1			2			2
20 June	2	5					1	1		1		2	1			3
25 June	2	6		1			2	2		1		2	1			4
30 June	5	7		1			3	3		1	1	3	1		1	6
5 July	10	8	4	5			4	4	1	1	3	4	2	1	2	8
10 July	13	10	9	9			4	5	3	2	5	7	3	1	2	6
15 July	14	13	10	13			6	7	3	3	8	7	4	1	4	6
20 July	14	15	11	14			8	10	3	4	9	9	6	2	5	6
25 July	14	15	12	14			8	11	3	4	9	9	8	1	5	7
30 July	13	15	11	14			8	9	5	4	10	9	7	2	7	4
4 Aug.	13	15	11	14			6	6	5	4	10	8	5	3	6	5
9 Aug.	15	13	14	12			6	8	5	4	10	6	4	5	5	3
14 Aug.	16	13	15	12			5	8	5	4	9	7	3	7	4	3
19 Aug.	16	13	14	12	1		2	6	3	5	8	7	2	9	6	4
24 Aug.	15	13	14	12	1		2	6	3	5	9	7	3	9	6	6
29 Aug.	14	14	13	13	1	1	2	6	2	4	8	6	3	9	7	4
3 Sept.	14	13	13	12	1	2	1	6	1	3	7	4	3	6	8	3
8 Sept.	11	11	11	10	1	2	1	3		1	6	5	2	3	6	3
13 Sept.	10	11	10	10	2	2	2	5		2	6	2	0	2	5	2
18 Sept.	10	11	10	10	2	2	1	5		2	5	1		2	3	3
23 Sept.	10	11	10	10	2	2	2	6		2	3	1		2	4	4
28 Sept.	9	11	10	10	3	2	2	6		1	2	1		2	5	2
3 Oct.	9	11	10	10	3	1	2	5		1	2	1		1	5	3
8 Oct.	8	10	8	9	2	1	2	5		1	1	1			5	3
13 Oct.	7	9	7	9	2		2	3			1				3	3
18 Oct.	7	6	6	6	2		2	2							2	2
23 Oct.	6	5	4	5	1			2							1	1
28 Oct.	2	2		2	1			1								
2 Nov.	1	2		2												

[a] Star. grack.—European Starling and Common Grackle; Br.-h. cowbrd—Brown-headed Cowbird; Red-wng. blkbd.—Red-winged Blackbird; Pur. mart.—Purple Martin; House sprw.—House Sparrow; Mourn. dove—Mourning Dove.

size from 2000 to more than 100,000 birds. The most abundant species in roosts were European Starlings and Common Grackles (Fig. 1). Secondary species, while present at varying times during the roosting season, constituted relatively small proportions of the total roosting population.

Population sizes for all species were very similar in both years, as were dates when secondary species were present in roosts (Fig. 1). In both years, the roosting season began in early June. In 1979 it built to a peak on 8 Sept., while in 1980 the peak occurred about a month earlier (19 Aug.). In both years, number of active roosts increased through the first half of the season and peaked at about the same time as population size (Table 1). Afterwards, population size and number of active roosts declined through the end of the local roosting season (Caccamise et al. 1983).

American Robins (*Turdus migratorius*) were the most abundant secondary species (Fig. 1), with juveniles forming a large and conspicuous part of all robin flocks that we encountered. In 1980 the number of robins declined markedly during late Aug. and early Sept. (Fig. 1). This coincided with a period of severe drought in the census area (N.O.A.A. 1980). A similar decline occurred for primary species, but, unlike starlings and grackles, numbers of robins present in roosts increased again soon after the first significant rainfall (17 Sept.).

Except for very early in the season, robins were present in nearly every active roost (Table 1). Maximum flock sizes for robins were as large as 20,000 (Fig. 2). Of the 40 roosts (both years) where robins were present, maximum flock sizes were usually larger than 100 (7 held >2000 robins, 6 held 1000–2000, 13 held 500–1000, 7 held 100–500, 8 held <100).

Red-winged Blackbirds (*Agelaius phoeniceus*) and Mourning Doves (*Zenaida macroura*), like robins, were also present for much of the season (Table 1). Their numbers were much lower, however, and they were present in fewer active roosts (Table 1, Fig. 2). We found examples of roosting flocks where each of these species (robin, red-wing, dove) was the primary species. Red-wings were primary species at two roosts in stands of common reed (*Phragmites communis*) along water courses within the study area. At one site where robins were numerous, they became the primary species when the roost was abandoned by starlings and grackles. We did not follow their activity after starlings and grackles left, but the population was clearly declining (Fig. 2, 1979, Roost 19).

The remaining secondary species were less widely distributed among roosts (Fig. 2). Flocks tended to be concentrated at a few sites, where they remained for relatively short intervals. For example, Brown-headed Cowbirds (*Molothrus ater*) occurred in only three roosts in 1979 and two in 1980 (Table 1, Fig. 2), but they were present in the study area over similar dates both years (Fig. 1).

Counts for Purple Martins (*Progne subis*) and House Sparrows (*Passer domesticus*) each included a small percentage (<10%) of Tree Swallows (*Tachycineta bicolor*) and House Finches (*Carpodacus mexicanus*), respectively. These data were combined, as we felt identifications were likely

unreliable given the poor light conditions and the often high rates of arrival for primary species.

Chimney Swifts (*Chaetura pelagica*) generally circled high over roost sites. They appeared specifically oriented to the sites, and were not simply present in the area. They apparently entered roosts, as we caught one in a mist net within the canopy of the roost vegetation (Lyon and Caccamise 1981).

Several secondary species were relatively uncommon (Fig. 1, bottom). Species like Green-backed Heron (*Butorides striatus*), Northern Mockingbird (*Mimus polyglottos*), and Northern Cardinal (*Cardinalis cardinalis*) were probably residents of woodlots where roosts were located. Although the American Crow (*Corvus brachyrhynchos*) is notorious for large roosting flocks, their numbers were always quite low in our roosts. In many areas Common Nighthawks (*Chordeiles minor*) begin migration as early as mid-Aug. (Selander 1954), which was when they appeared in our roosts during both years of the study.

DISCUSSION

Secondary species can be overlooked easily when roosting populations are large and primary species are conspicuous. We found secondary species, however, in nearly every roost examined. This was true throughout the season and for all roost sizes. Although each species had a unique pattern of association, their presence together resulted in considerable heterogeneity in species composition throughout the roosting season.

In presenting the information center hypothesis, Ward and Zahavi (1973) were unable to find any evidence that mixed species roosting flocks included species with dissimilar foods or feeding places, except where roost sites were limited. By providing support for our first hypothesis, we have shown that this was not the case in our study area. Many secondary species have foraging requirements quite distinct from other species in the roosts. For these, interspecific exchange of foraging information appears an unlikely reason to form mixed species roosting flocks (e.g., House Sparrows, Mourning Doves, Red-winged Blackbirds, and Purple Martins).

For other species, determining the potential for interspecific exchange of foraging information is more difficult (e.g., grackles and starlings). This is because we do not know how similar foraging requirements must be in order for foraging benefits to be possible. For example, in our study

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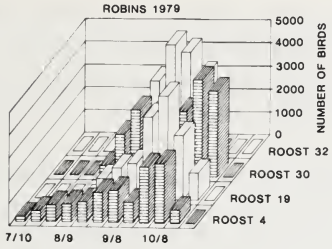
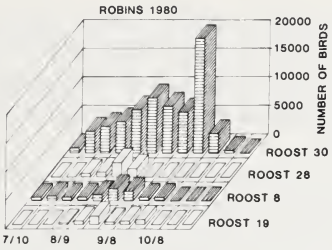
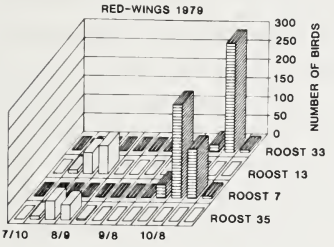
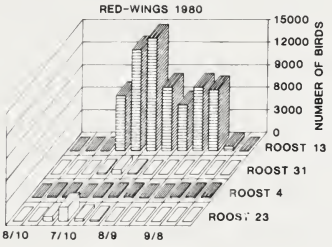
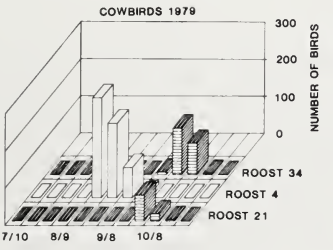
FIG. 2. Seasonal patterns in roosting flock size at individual roosts. Roosts depicted for each secondary species were those with the largest population sizes.

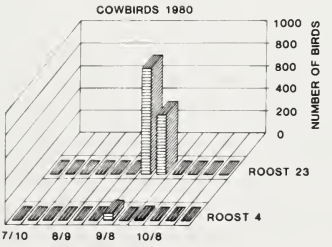

ROBINS 1979
5000
4000
3000
2000
1000
0
NUMBER OF BIRDS
ROOST 32
ROOST 30
ROOST 19
ROOST 4
7/10
8/9
9/8
10/8

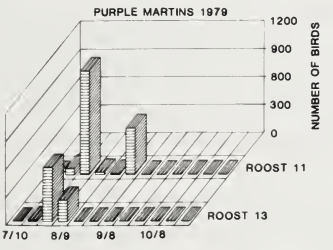

ROBINS 1980
20000
15000
10000
5000
0
NUMBER OF BIRDS
ROOST 30
ROOST 28
ROOST 8
ROOST 19
7/10
8/9
9/8
10/8

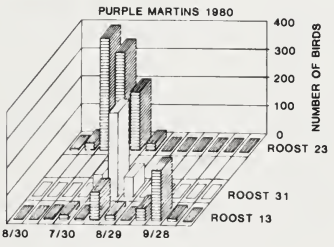

RED-WINGS 1979
300
250
200
150
100
50
0
NUMBER OF BIRDS
ROOST 33
ROOST 13
ROOST 7
ROOST 35
7/10
8/9
9/8
10/8

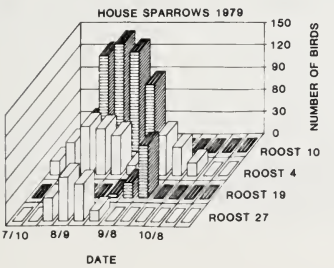

RED-WINGS 1980
15000
12000
9000
8000
3000
0
NUMBER OF BIRDS
ROOST 13
ROOST 31
ROOST 4
ROOST 23
8/10
7/10
8/9
9/8

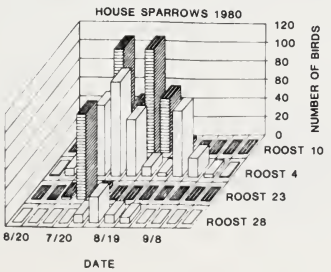

COWBIRDS 1979
300
200
100
0
NUMBER OF BIRDS
ROOST 34
ROOST 4
ROOST 21
7/10
8/9
9/8
10/8


COWBIRDS 1980
1000
800
800
400
200
0
NUMBER OF BIRDS
ROOST 23
ROOST 4
7/10
8/9
9/8
10/8


PURPLE MARTINS 1979
1200
900
800
300
0
NUMBER OF BIRDS
ROOST 11
ROOST 13
7/10
8/9
9/8
10/8


PURPLE MARTINS 1980
400
300
200
100
0
NUMBER OF BIRDS
ROOST 23
ROOST 31
ROOST 13
8/30
7/30
8/29
9/28


HOUSE SPARROWS 1979
150
120
90
80
30
0
NUMBER OF BIRDS
ROOST 10
ROOST 4
ROOST 19
ROOST 27
7/10
8/9
9/8
10/8
DATE


HOUSE SPARROWS 1980
120
100
80
80
40
20
0
NUMBER OF BIRDS
ROOST 10
ROOST 4
ROOST 23
ROOST 28
8/20
7/20
8/19
9/8
DATE

area Common Grackles occurred in less than 10% of starling foraging flocks observed over a period of 17 months (Fischl 1983). It is open to conjecture whether or not foraging requirements of these species are sufficiently distinct to preclude foraging benefits as a basis for mixed species roosting.

In our second hypothesis we predicted that, for some species, numbers of individuals in roosting flocks were sufficiently large to maximize predator protection (e.g., Lack 1968, Gadgil and Ali 1976) without the need to form mixed species flocks. Pulliam (1973) pointed out that relationships between levels of predator protection and group size are likely asymptotic, with maximum benefits achieved at relatively small group sizes (<100). In addition, costs increase with flock size because of increased commuting distances and greater competition for favored positions at both roost sites (Swingland 1977) and in foraging areas (Hamilton and Gilbert 1969).

In our study, size of single-species aggregations (within mixed roosting flocks) varied greatly among roosts (Fig. 2). The more abundant species (e.g., robins) occurred in large numbers at active roosts throughout the study area. For these species aggregations were much larger than the minimum size required for maximizing predator protection. Flock sizes for less abundant species (e.g., Purple Martins, House Sparrows) also were often large enough to maximize predator protection, because they aggregated at few sites generally forming relatively large roosting flocks. Thus, for most secondary species, predator protection alone does not appear to explain the formation of mixed species roosting flocks.

Many factors likely influence an individual's choice of a night time roosting site. Our results, however, lead to the conclusion that neither limited availability of roost sites (Caccamise et al. 1983) nor information exchange (Ward and Zahavi 1973) offer suitable explanations for the presence of some species in our roosting flocks. Also, it appears, on theoretical grounds (Pulliam 1973), that predation protection does not alone offer a satisfactory explanation.

The security offered by roosting sites certainly must be an important part of the site selection process. Protection from predators, however, is only one of many factors influencing the security and overall quality of roost sites. Individuals must select sites based on many features, including absence from disturbance, protection from weather events, and proximity to feeding areas. Typically, roosting activity begins with a small group, which increases in size over periods ranging from days to months, with individual sites often used for many years (Caccamise et al. 1983). Therefore, the factors influencing site quality appear to be generally stable over time.

An individual or group seeking a roost site can avoid risks of making a poor selection by choosing to roost at an established site. This feature might be particularly important to young of the year or transients moving through an area. Both groups would be unfamiliar with local conditions and could benefit by selecting a site of established quality. In this way active sites would attract individuals of many species because they are secure and provide some assurance that at least minimum requirements will be met. This could lead to development of very large roosting flocks made up of species having little apparent basis for commonality (e.g., Common Nighthawks, Brown-headed Cowbirds).

This concept broadens the conventional view of predator protection by considering the importance of (1) risks from a variety of sources; and (2) overall quality of roost sites. It also provides an explanation—at least in part—for why roosts are often large and contain a variety of different species. Minimizing risks associated with the selection of roost sites, however, does not offer an explanation for why roosts form in the first place.

SUMMARY

This study examines population dynamics of secondary species associated with roosts composed primarily of European Starlings (*Sturnus vulgaris*) and Common Grackles (*Quiscalus quiscula*). Our goal was to determine patterns of association for secondary species and to evaluate the role of interspecific relationships in roosting flocks. We estimated sizes of roosting populations over 2 seasons for all roosts within a large census area. From June to November roosts were active 3–20 weeks and varied in size from 2000 to over 100,000 individuals. We found 17 secondary species; numbers ranged from fewer than 10 individuals (Green-backed Heron, *Butorides striatus*) to over 20,000 (American Robin, *Turdus migratorius*). They were in nearly every roost, irrespective of season or roost size. Although each species had a unique pattern of association, their presence together resulted in considerable species heterogeneity.

For those roosting species with distinct foraging requirements, interspecific exchange of foraging information is an unlikely reason to form mixed species roosting flocks. Also, species that form large (>100) roosting flocks apparently do not join mixed species flocks only for added predator protection, as these benefits are likely asymptotic at relatively small flock sizes. There are many factors that make roost sites attractive. By selecting occupied roosts, individuals can lower the risk of choosing poor sites, and be assured that, at least, minimum requirements will be met. This concept provides an explanation for why very large roosting flocks develop, and why they are often composed of species with little apparent basis of commonality.

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Wilson Bull., 97(2), 1985, pp. 183–190

BREEDING ROBINS AND NEST PREDATORS: EFFECT OF PREDATOR TYPE AND DEFENSE STRATEGY ON INITIAL VOCALIZATION PATTERNS

Bradley M. Gottfried, Kathryn Andrews, and Michaela Haug

Breeding birds are subject to intense nest-predation pressure by a variety of predators (Gottfried 1978, Gottfried and Thompson 1978). To counteract this pressure, a number of antipredator adaptations have evolved in birds. These adaptations appear to involve nest concealment, distraction displays, and colonial nesting (Skutch 1976). Another antipredator strategy is active nest defense. By imposing the possibility of injury on a predator, a breeding bird may be successful in protecting its nest. Indeed, experimental studies have shown that nesting birds do attack models of nest predators (see Gottfried 1979 and references cited therein). As expected, the intensity of defense increases through the breeding cycle as the amount of parental investment increases (Shields 1984). There is also evidence that birds respond in a different manner to different types of nest predators (Gottfried 1979).

Actual fighting between two animals can be costly in terms of risk of physical injury as well as in time and energy. It has been hypothesized that mechanisms have evolved to reduce the incidence of these interactions (Maynard Smith 1974). As most contests are asymmetric (e.g., the contestants are not equally matched), it is important for each contestant to assess the likelihood that it will win a contest. If, after assessing the situation, a contestant finds that its chances of winning an encounter are low, it may well forgo further interaction, and retreat (Parker 1974). Threat displays may be an important cue in determining the formidability of a particular opponent. Another potential source of information about an opponent may be in its repertoire of vocalizations. Smith (1977) has shown that auditory signals have evolved as an effective way of transmitting information among organisms. Alternative explanations have also been offered (Dawkins and Krebs 1978).

Birds possess a unique repertoire of sounds that are used in territory defense, courtship, and flock maintenance; and a number of studies have shown that birds have the ability to use vocalizations to convey contextual information about motivation levels. Vocalizations conceivably could be used by a nest predator in assessing motivation levels and defense strategy of a breeding bird, or they could be used to signal information about predator-type and form of defense strategy to conspecifics and thus could be used to coordinate nest defense. Predator-induced vocalizations have

been studied extensively in ground squirrels. These organisms give predator-specific types of alarm calls that may also encode information about the predator's activity patterns (Owings and Virginia 1978, Leger et al. 1980, Owings and Leger 1980, Robinson 1980). There have been few similar studies of birds, and most were not experimental (Morton and Shalter 1977, Greig-Smith 1980).

This paper reports on a study in which we examined the vocalizations of American Robins (*Turdus migratorius*) in relation to models of two types of nest predators. We were particularly interested in determining whether initial vocalizations accurately reflected later nest defense strategies (attack or not attack the model), and in the type of predator eliciting the calls.

METHODS AND MATERIALS

The study was conducted from April through July in 1980 and 1981 in old-field habitats in and around St. Paul, Minnesota. We attempted to locate nests soon after egg laying was initiated. Each nest was tested three to five days after the start of incubation. The following technique was used for each test. A stuffed Blue Jay (*Cyanocitta cristata*) or a rubber snake model was affixed to the nest after the female left to feed. After positioning the predator, we retreated to a concealed position approximately 15 m away, from which we could observe subsequent events at the nest. Each test lasted about five min. We used a Uher 4000 Report Moniter tape recorder and a Dan Gibson P650 microphone to record the vocalizations. The tapes were later analyzed with a Kay sonograph model 6061B. In all tests, the vocalizations uttered by the female within five sec of its return to the nest were analyzed. These vocalizations were referred to as the Initial Response Repertoire (IRR). The response of the nesting bird to the predator model was also ranked using the scale presented in Table 1.

RESULTS

Robins primarily used two types of vocalizations in their responses to predator models (Fig. 1): "chirps" and "chucks." "Chirps" were more complex than "chucks," being longer in duration and composed of a wider range of frequencies.

The type of predator model presented influenced the type of vocalization included in a bird's IRR. Eighty-eight percent of the robins tested with the stuffed Blue Jay included "chirps" in their IRR, but only 42% uttered "chirps" in response to the snake ($\chi^2 = 8.62$, df = 1, $P < 0.05$). The proportion of robins that included "chucks" in their IRR to the jay was not significantly different from those that included "chucks" to the snake ($\chi^2 = 0.39$, df = 1, $P < 0.05$).

"Chirps" were significantly more likely to be included in the IRR of birds that ultimately attacked a model than those that did not attack (92% vs 41%; $\chi^2 = 8.29$, df = 1, $P < 0.05$). "Chucks," on the other hand, were more likely to be included in the IRR of robins that did not later attack the predator models (73% vs 38%; $\chi^2 = 4.82$, df = 1, $P < 0.05$).

TABLE 1
SCALE USED TO DETERMINE THE AGGRESSION RESPONSE INDEX OF ROBINS

Aggression	Movement pattern
0 = No response	0 = No movement
1 = Approach predator (<5 approaches and retreats/min) no attacks	1 = Little movement (<5 changes in position/min)
2 = Frequent approaches (>5 approaches and retreats/min) no attacks)	2 = Medium movement (>5–30 changes in position/min)
3 = Few attacks (<5 strikes on predator/min)	3 = Frenzied movement (>30 changes in position/min)
4 = Frequent attacks (>5 strikes on predator/min)	

Robins that ultimately attacked a jay model were more likely to utter "chirps" than birds that did not attack the jay ($\chi^2 = 5.03$, df = 1, $P < 0.05$; Table 2), while "chucks" were more likely to be given by birds that did not later attack the jay models than by those birds that did ($\chi^2 = 3.71$, df = 1, $P < 0.05$). Too few robins attacked the snake model to permit a statistical analysis of the data.

To explore the fine details of the "alarm" vocalizations, sonograph tracings were made, and data were collected and subsequently analyzed using 2 × 2 Analyses of Variance (ANOVA) in an effort to examine possible differences.

The two main effects in the ANOVA were predator type and ultimate form of defense. Three of the seven vocal parameters studied were significantly related to the type of predator model presented (Table 3). Robins uttered twice as many vocalizations/30 sec (particularly "chirps") in response to the jay model as they did to the snake. This was caused by significant differences in the number of "chirps"/30 sec; the number of "chucks"/30 sec was not affected. The increase in the number of vocalizations/30 sec was at the expense of the duration of intervals between notes and not in note length. The ANOVA suggests that the quantitative changes in the IRR in relation to ultimate defense strategy somewhat parallel that of predator type, with birds that later attacked the model uttering significantly more notes in general, and "chirps" in particular, than birds that did not ultimately attack the model.

Robins that ultimately attacked the jay model included a significantly greater number of vocalizations/30 sec in their IRR than those birds that did not attack the model (Table 3). These pre-attack vocalizations con-

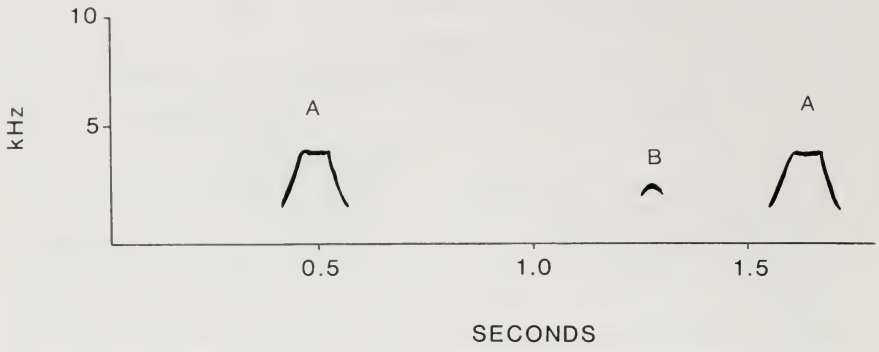

FIG. 1. Sample sonograph tracing of a robin vocalization. Notes with an A are "chirps", those with a B are "chucks."

tained significantly more "chirps" and fewer "chucks" than those robins that did not attack the jay model. Robins that ultimately attacked the jay model also uttered "chucks" whose frequency was significantly different from those birds that did not attack the model.

The IRR of robins that ultimately attacked the snake model contained significantly more notes/30 sec and significantly more "chucks" than the IRR of robins that did not attack the snake. The attacking robins also gave shorter "chirp" vocalizations than robins that did not later attack.

The IRR of robins prior to attacks on the jay and snake models did not contain significantly different numbers of vocalizations/30 sec. This was due to significant but opposite trends in the number of "chirps" and "chucks" (Table 3). Robins that later attacked the jay model uttered an average of 60.3 "chirps"/30 sec, compared to only 20.5/30 sec in those that later attacked the snake. On the other hand, the number of "chucks"/30 sec was 41.8 in the snake experiments and only 1.1 in the jay experiments. Attacks on the jay model were also preceded by "chirps" that contained a shorter time interval between notes than those in the IRR which preceded attacks on the snake model.

The data presented so far indicate that several vocal parameters, particularly the number of vocalizations/30 sec, are related to defense strategy. As the intensity of the responses to the model varied, the data were analyzed with a Spearman Rank Correlation Test to determine if any of the seven vocal parameters was correlated with intensity of nest defense. The intensity of defense was correlated positively with the total number of vocalizations/30 sec ($r_s = 0.76$, $P < 0.05$), the number of "chirps"/30 sec ($r_s = 0.75$, $P < 0.05$), and low ($r_s = 0.57$, $P < 0.05$) and high ($r_s = 0.58$, $P < 0.05$) frequency of "chirps". Duration of "chirps" ($r_s = 0.33$,

TABLE 2
NUMBER OF AMERICAN ROBINS UTTERING "CHIRPS" AND "CHUCKS" IN RELATION TO PREDATOR AND LIKELIHOOD OF ATTACK

Predator model	N	No. giving "chirps" (%)	No. giving "chucks" (%)
Blue Jay			
Attack	22	22 (100)	6 (27)
No attack	10	6 (60)	10 (100)
Total	32	28 (88)	16 (50)
Snake			
Attack	4	2 (50)	4 (100)
No attack	20	8 (40)	6 (30)
Total	24	10 (42)	10 (42)

$P > 0.05$) or their spacing ($r_s = 0.45$, $P > 0.05$) were not correlated with the levels of aggression.

DISCUSSION

Our results suggest that certain parameters, specifically the number of vocalizations a robin utters, the number of major vocalization types ("chirps"), and certain frequency parameters are related to predator type, future defense decisions, and the intensity of future nest defense.

These results are consistent with earlier studies of monkeys and ground squirrels. Vervet Monkeys (*Cercopithecus aethiops*) possess large repertoires of predator-specific alarm calls (Struhsaker 1967, Cheney and Seyfarth 1981). Broadcast of these signals caused free-ranging monkeys to take appropriate defensive measures (Seyfarth et al. 1980). The vocal signals of ground squirrels, although lower in diversity, also show evidence of being predator-specific (Owings and Virginia 1978, Robinson 1980). For example, California Ground Squirrels (*Spermophilus beecheyi*) emit "chatters" and "chats" in the presence of terrestrial predators, and "whistles" when raptors are present. Detailed spectrographic examination of vocalizations was conducted by Owings and Leger (1980) and Leger et al. (1980). "Chatters" evoked by raptors and terrestrial predators were distinct from each other. Owings and Leger (1980) also found the rate of calling to be related to the type of predator. Ground squirrels communicate predator identity through the use of predator-specific vocalization, graded signals, and rates of calling. These data agree with those we collected on robins. Robins were more likely to emit "chirps" than "chucks" in response to the jay model, but were equally likely to utter "chirps" and

TABLE 3

RESULTS OF AN ANOVA OF THE EFFECT OF PREDATOR TYPE AND FUTURE DEFENSE STRATEGY ON VARIOUS VOCALIZATION VARIABLES OF ROBINS

	Main effects						Subeffects							
	Fate			Predator			Means				F Values			
Variable	Attack $\bar{x}$	No attack $\bar{x}$	F	Blue Jay $\bar{x}$	Snake $\bar{x}$	F	Snake/ attack $\bar{x}$	Snake/ no attack $\bar{x}$	Blue Jay/ attack $\bar{x}$	Blue Jay/ no attack $\bar{x}$	Attack BJ vs snake	No attack BJ vs snake	Blue Jay attack vs no attack	Snake attack vs no attack
Sample size	26	30		32	24		4	20	22	10				
Number of vocalizations/ 30 seconds	58.6	20.4	19.1[a]	54.4	22.4	6.7[a]	50.0	13.3	61.4	37.7	1.7	7.9[a]	7.5[a]	17.9[a]
Number of "chirps"/30 sec	50.3	10.8	24.6[a]	45.7	13.3	11.0[a]	20.5	10.9	60.3	10.7	28.3[a]	0.1	43.9[a]	6.1[a]
Number of "chucks"/30 sec	11.3	8.8	2.5	7.8	12.1	3.3	41.8	2.3	1.1	24.5	40.9[a]	12.2[a]	13.5[a]	38.6[a]
Interval between notes (msec)	205.8	222.2	0.39	188.4	210.3	11.4[a]	285.0	191.4	262.4	182.0	9.4[a]	7.0[a]	0.6	0.1
Duration of "chirps" (msec)	83.7	89.6	2.1	83.8	91.5	2.1	82.0	83.9	93.4	83.3	0.3	7.3[a]	0.1	9.3[a]
Low frequency of "chirps" (kHz)	1.4	1.4	0.5	1.4	1.4	0.3	1.5	1.4	1.4	1.3	0.6	0.6	0.6	0.6
High frequency of "chirps" (kHz)	4.4	4.3	3.5	4.4	4.4	0.7	4.6	4.5	4.4	4.3	1.0	1.0	4.0[a]	4.0[a]

[a] Significant at $P < 0.05$.

"chucks" to the snake. Our study suggests that the ultimate defense strategy (attack or not attack) and intensity of future defense may be encoded in a robin's predator-induced vocalizations. In addition to the quantitative data presented, this idea is supported by qualitative observations at robin nests. In most of the tests where the robins ultimately attacked the predator models, their vocalizations attracted other robins as well as Common Grackles (*Quiscalus quiscula*) and Field Sparrows (*Spizella pusilla*) to the area around the nest. Breeding robins tended to attack these new arrivals, but were usually unable to drive them away. We conducted similar predator-induced vocalization studies with Gray Catbirds (*Dumetella carolinensis*). During these tests, other catbirds were attracted by the vocalizations of the nesting catbird being tested, but unlike robins, these arrivals were tolerated and they may have been involved in attacking the predator models. Robins and catbirds that did not ultimately attack the predator model did not attract other birds to the general area around their nests. By uttering certain numbers and types of vocalizations a bird might be able to gain assistance from other birds in the area in its defense against the predator. Even in our observations of robins where other birds were not involved in defense, the presence of additional agitated birds may be enough to dissuade a predator from continuing its attempt to prey on the contents of the nest.

SUMMARY

The study was conducted to determine if predator-induced vocalizations of breeding American Robins (*Turdus migratorius*) were related to predator identity (Blue Jay [*Cyanocitta cristata*] or snake), later defense strategy (attack or not attack model), and intensity of future defense. Robins used two types of vocalizations in their response to the nest predators: "chirps" and "chucks."

Nesting robins were significantly more likely to utter "chirps" than "chucks" in tests with a stuffed Blue Jay. All birds that later attacked the jay included "chirps" in their repertoire; all those that did not attack included "chucks" in their repertoire. In experiments with a snake model, both types of vocalizations were equally likely to be given. The number of vocalizations/30 sec and the number of "chirps"/30 sec were consistently related to predator type, future defense strategy, and intensity of future defense.

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AGGREGATIONS OF CORY'S SHEARWATERS (*CALONECTRIS DIOMEDEA*) AT GULF STREAM FRONTS

J. Christopher Haney and Philip A. McGillivary

Seabirds are adapted to marine communities where prey concentrations are patchy and short-lived. Hydrographic events and physical properties of water masses combine to influence the distribution and abundance of lower trophic level prey organisms. These processes may also account for some, and occasionally most, of the variation in the abundance and distribution of seabirds. Seabird faunas have been related to sea-surface temperature (Murphy 1936, Bourne *in* Palmer 1962, Ashmole 1971, Watson 1975) or to water masses defined by surface temperature and salinity (Pocklington 1979), and several investigators have related the distribution of individual seabird species to sea-surface temperature and major current systems (e.g., Szijj 1967, Jehl 1973, Gould 1983). However, few studies have correlated smaller-scale variation in seabird abundance with the distribution of physical processes (e.g., Brown 1980a). Recently, oceanographic research on specific hydrodynamic features has enabled ornithologists studying marine birds to investigate and interpret such interactions simultaneously (Brown 1980b).

Hydrographic fronts that occur at adjoining water masses of differing densities (temperature and/or salinity) are one example of small-scale physical oceanographic events (Stommel 1963, Haury et al. 1978), and seabirds have been associated with fronts at the edge of the continental shelf in the Bering Sea (Kinder and Coachman 1978, Iverson et al. 1979, Schneider 1982, Kinder et al. 1983), Ross Sea (Ainley and Jacobs 1981), and Northwest Atlantic (Brown 1977, Fournier 1978, Orr et al. 1982). The association of seabirds with fronts in the South Atlantic Bight region (Cape Hatteras, North Carolina to Cape Canaveral, Florida) has not been reported previously.

Cory's Shearwaters (*Calonectris diomedea*) inhabit warm temperate and subtropical seas and breed north of the equator on islands of the eastern Atlantic and Mediterranean (Cramp and Simmons 1977). Nonbreeders disperse to the western Atlantic, including the continental shelf of the southeastern United States, during summer and fall (Clapp et al. 1982). Here, we present evidence that Cory's Shearwaters aggregate at Gulf Stream surface thermal fronts during summer and fall at the shelf break in the southern portion of the South Atlantic Bight. We offer hy-

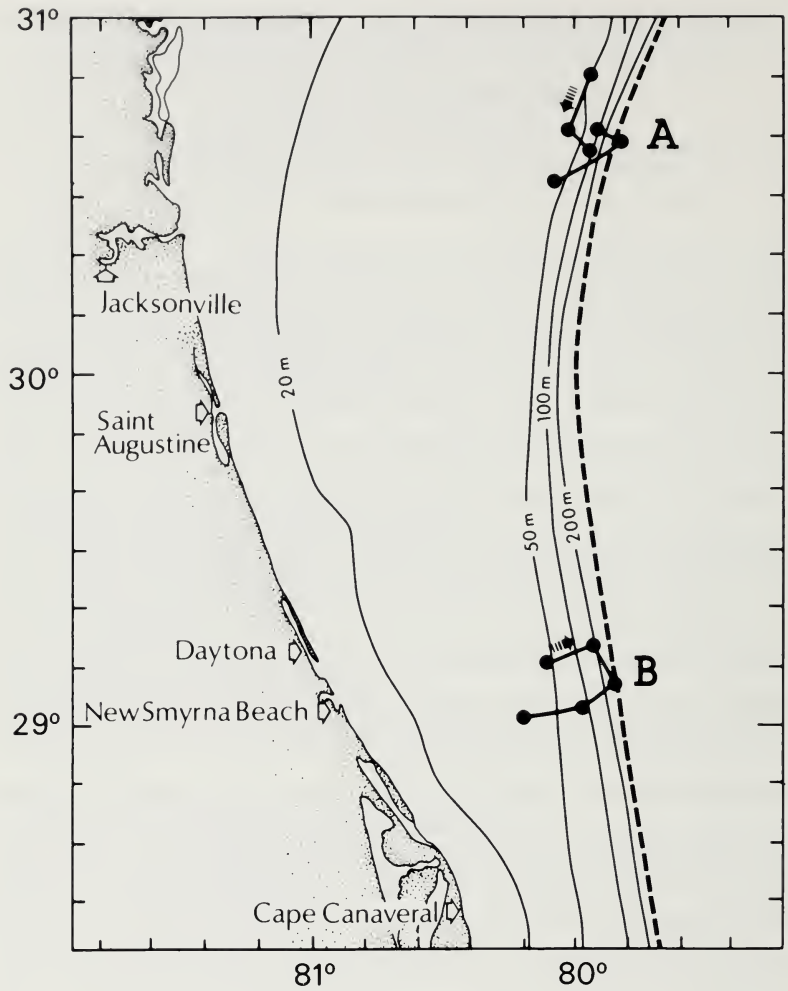

FIG. 1. Map of southern South Atlantic Bight with 13 July 1983 (A) and 1 Oct. 1983 (B) cruises indicated with arrows. Annual mean position of western Gulf Stream surface thermal front is shown by dashed line. Depth contours are indicated by solid lines.

potheses to explain why these aggregations occur, and discuss the possible relationships of hydrographic structure to biological processes at the front.

METHODS

Study area.—Research was conducted in the southern South Atlantic Bight region off northeast Florida and southeast Georgia (Fig. 1). The region is characterized by a wide, shallow continental shelf that narrows considerably at the southern and northern extremes

TABLE 1

SPECIES COMPOSITION OF SEABIRDS OBSERVED DURING JULY AND OCTOBER 1983 SURVEYS OF THE SOUTH ATLANTIC BIGHT OUTER SHELF

	July			October		
	N	% of transects observed on	% of all birds seen	N	% of transects observed on	% of all birds seen
Calonectris diomedea	81	36	82	199	50	98
Puffinus lherminieri	6	16	6	3	50	1
Phaethon lepturus	1	4	1	0	0	0
Sterna maxima	1	4	1	0	0	0
Sterna hirundo	1	4	1	0	0	0
Sterna anaethetus	8	8	8	2	33	1
Sterna spp.	1	4	1	0	0	0

near Cape Canaveral, Florida, and Cape Hatteras, North Carolina. In this region, surface-slope waters are absent and warm oceanic (i.e., Gulf Stream) water interacts directly with shelf waters. Mixing regimes segregate shelf waters into inner-shelf (0–20 m), middle-shelf (20–40 m), and outer-shelf (40–200 m) domains. The climatology of these water masses is summarized by Atkinson et al. (1983). Transects were carried out in the outer shelf domain where variations in Gulf Stream frontal effects, occurring on time scales of 2 to 14 days, are as large as seasonal variations (Lee and Atkinson 1983). Over the outer continental shelf a southeasterly drift predominates during summer and fall. At the shelf break, however, surface currents are to the northeast due to frictional interaction with the Gulf Stream (Bumpus 1973).

Bird counts.—Counts of seabirds, including Cory's Shearwaters, were made during bi-monthly surveys of the seabird fauna of the South Atlantic Bight. Observations reported here are from cruises made on 11–15 July 1983 aboard the 21-m R/V "Bluefin" (Skidaway Institute of Oceanography) and on 29 Sept.–13 Oct. 1983 aboard the 41-m R/V "Cape Hatteras" (Duke University Marine Lab). Simultaneous oceanographic measurements and seabird counts across and along the western Gulf Stream front were made on 13 July and 1 Oct. during the respective periods of these cruises (Fig. 1).

Observations of seabirds were recorded during 15-min periods (one 15-min count = one transect). Transects were made while the vessel proceeded on a constant course and heading. Ship speed during transects varied from 4.3 to 8.3 knots (6.3 to 15.3 km/h). Ship location and speed were recorded at the beginning and end of each transect. Transects were continuous and consecutive during counts across and along the front to increase spatial resolution of physical events and seabird concentrations.

All birds were counted out to a distance of 300 m from the observer within a 90° sector on the side of the ship with less sun glare. Distance was determined with a hand-held fixed-interval rangefinder made from a modified set of calipers (Heinemann 1981). Birds not in the transect zone of 300 m were counted but were not included in density estimates. Birds flying into the transect zone from the stern were excluded to avoid bias from individuals following the ship. One individual (Haney) did all of the counting.

Physical measurements.—For chlorophyll measurements, a Model 10-070 Turner Design flow-through fluorometer with infrared sensitive photomultiplier was used with a standard Blue lamp and 5–60 excitation/2–54 emission filter assembly specific for chlorophyll *a*

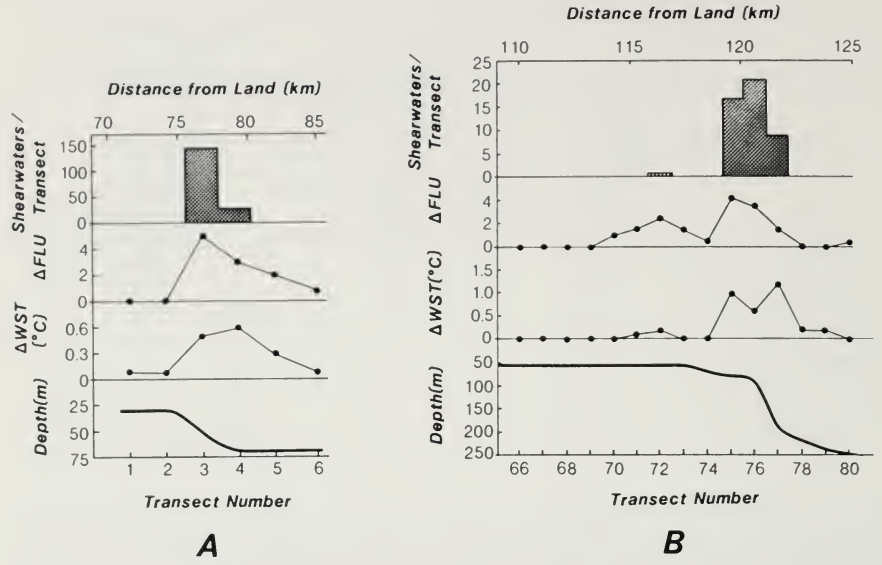

FIG. 2. Relationship of Cory's Shearwater abundance to environmental changes at Gulf Stream surface thermal front on 1 Oct. 1983 (A) and 13 July 1983 (B).

(Strickland and Parsons 1972). Seawater was obtained from a through-hull pumping system with intake at a depth of three m. Water was directed through a debubbler before it entered the fluorometer. Because all readings were made during daylight hours (0700–1500 EDT), no corrections are made for day–night changes in fluorescence to chlorophyll *a* ratios (cf. Kiefer 1973). Simultaneous temperature measurements were obtained with a towed Wheatstone bridge thermistor. Temperature and fluorescence measurements were recorded simultaneously on a Esterline-Angus MS-412B Mini–Servo chart recorder. Concurrent depth measurements were made with a SIMRAD EL fathometer set to two m sensitivity scale.

Data analyses.—Seven environmental variables were compared to an index of the abundance of Cory's Shearwaters (birds/transect). Depth (DEP) and change in depth (ΔDEP) were measured to the nearest two m for each transect. Distance from land (DFL) and distance from the Gulf Stream front (DFF) were measured to the nearest two km using NOAA Gulf Stream System Flow Charts obtained from infrared satellite data. The temperature of the water surface (WST) and change in water surface temperature (ΔWST) were measured to the nearest 0.1°C. Change in fluorescence (ΔFLU) was calculated to the nearest 0.1 relative fluorescence unit (Strickland and Parsons 1972).

Relationships among the seven environmental variables and between these variables and the abundance of Cory's Shearwaters were assessed with correlation analysis (r). The data were not transformed. The non-parametric Mann-Whitney U-test was used to test for significant differences between Cory's Shearwater abundance in near-front (<4 km from the front) and other transects (≥4 km from the front). For the purposes of this test the front was defined as that location with the highest change in water surface temperature (transect 77 on 13 July and transect 4 on 1 Oct.). Statistical significance was set at $P < 0.05$.

RESULTS

Cory's Shearwater was the dominant species of seabird recorded during the two cruises, constituting 82% of all seabirds seen on 13 July (N = 25

TABLE 2

CORRELATIONS OF THE ABUNDANCE OF CORY'S SHEARWATERS (BIRDS/TRANSECT) AND ENVIRONMENTAL VARIABLES MEASURED ON 13 JULY 1983 CRUISE TRACK (DF = 23)

Variable	r	P	$\bar{x} \pm$ SD	Range
DEP[a]	0.14	NS	144 ± 77	50–250
ΔDEP	−0.03	NS	12 ± 19	0–80
DFL	0.12	NS	115 ± 5	108–126
DFF	−0.46	<0.05	5.3 ± 3.8	0.0–16.0
WST	0.05	NS	27.8 ± 0.8	26.7–29.0
ΔWST	0.87	<0.001	0.2 ± 0.4	0.0–1.3
ΔFLU	0.54	<0.01	0.9 ± 1.2	0.0–4.2

[a] Abbreviations are explained in the text.

transects) and 98% of the total on 1 Oct. (N = 6) (Table 1). It was the only species exhibiting significant relationships to the Gulf Stream front.

Variance among counts of Cory's Shearwaters was high. Shearwater abundance varied from 0 to 24 birds/transect ($\bar{x}$ = 3, SD = 7, N = 25) on 13 July and from 0 to 146 birds/transect ($\bar{x}$ = 29, SD = 58, N = 6) on 1 Oct. Density varied from 0 to 42 birds/km^2 ($\bar{x}$ = 5, SD = 12, N = 25) on 13 July and 0 to 97 birds/km^2 ($\bar{x}$ = 19, SD = 39, N = 6) on 1 Oct.

On 13 July and 1 Oct., aggregations of Cory's Shearwaters occurred at or near the Gulf Stream surface thermal front where the changes in water surface temperature and fluorescence values were highest (Fig. 2). On 13 July, correlations of shearwater abundance to environmental variables were significant for distance from front, change in water surface temperature, and change in fluorescence (Table 2). These three variables ac-

TABLE 3

CORRELATION MATRIX OF ENVIRONMENTAL VARIABLES MEASURED DURING 13 JULY 1983 CRUISE TRACK[a]

Variable	DEP	ΔDEP	DFL	DFF	WST	ΔWST
ΔDEP[b]	0.25					
DFL	0.73***	0.44*				
DFF	−0.41*	−0.09	−0.39			
WST	0.81***	0.32	0.76***	0.01		
ΔWST	0.32	0.07	0.22	−0.40*	0.54**	
ΔFLU	−0.06	−0.14	−0.46*	−0.43*	−0.06	0.44*

[a] Significance levels indicated as follows: * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$), df = 23.
[b] Abbreviations are explained in the text.

counted for 21%, 76%, and 29%, respectively, of the variance in shearwater abundance. On 1 Oct., shearwater abundance was significantly correlated only with change in fluorescence ($r = 0.873$, df = 4, $P < 0.05$), which accounted for 76% of the variance in shearwater abundance. Environmental changes associated with the Gulf Stream surface thermal front showed marked intercorrelations (Table 3).

Density along near-front transects averaged 14.9 birds/km^2 vs 0.7 birds/km^2 elsewhere on 13 July and 37.7 birds/km^2 vs 0.0 birds/km^2 elsewhere on 1 Oct. Average abundance (birds/transect) of Cory's Shearwater on 13 July in near-front transects was significantly higher than in other transects (9.5 vs 0.2; $P < 0.01$, Mann-Whitney *U*-test, N = 8, 17, $z = 3.82$). On 1 Oct., average shearwater abundance was higher than in other transects, but not at the 5% significance level (87.0 vs 0.0; $P < 0.07$, Mann-Whitney *U*-test, N = 2, 4, $z = 1.62$).

DISCUSSION

Elevated levels of biological activity at fronts have been observed previously (Pingree et al. 1974, Floodgate et al. 1981, Owen 1981, Vinogradov and Shushkina 1983), and we suggest that the association of Cory's Shearwaters with the Gulf Stream surface thermal front is due to enhanced food availability. The biology of *C. diomedea* and the circulation at Gulf Stream fronts are examined in an attempt to explain further this relationship.

Physical processes occurring at the fronts were visually striking on both dates counts were conducted. The Gulf Stream side was smooth while the shelf side had capillary waves. On both occasions winds were light (< 5 knots) and oriented alongshore from the south prior to and during the study periods. The cross-shelf dimensions of the fronts were <100 m at the surface. Current shear appears to account for the physical and biological phenomena observed.

Steady wind stress can produce three-dimensional circulation if the bottom topography contains a discontinuity in gradient (Hill and Johnson 1974). Such a discontinuity can be merely a 2.6 m/10 km change in depth across the shelf. This was evident at both shelf break locations (Fig. 2). Above the edge of the shelf a convergence shear front forms and vertical transport may occur over very small horizontal distances (Fig. 3). A sharp lateral current shear associated with the thermohaline mixing regime between Gulf Stream and outer-shelf water has been documented previously by remote sensing (Maul and Hansen 1972). The dynamics of such shelf break fronts have been discussed further by Csanady (1973), Mooers et al. (1976), and Garvine (1980).

Turbulence and vertical transport in shear fronts may entrain organisms

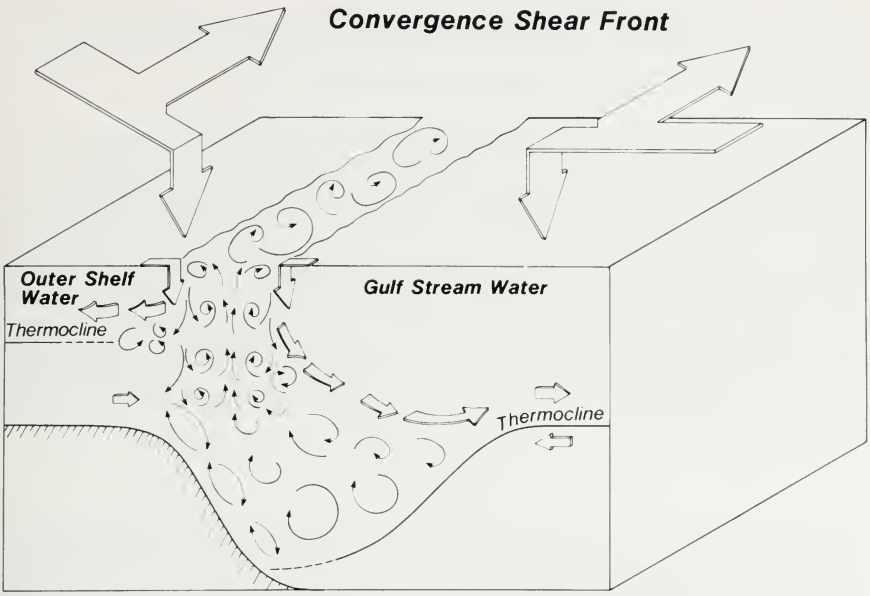

FIG. 3. Simplified representation of lateral convergence shear front at the continental shelf break. The width of the shear layer has been exaggerated to show the details of the circulation. The higher velocity of the Gulf Stream results in alongshelf turbulent dynamics that are not depicted. Typical thermocline depths are 25–40 m (outer shelf) and 75–100 m (Gulf Stream).

from depths where they would not normally be available to surface foragers. Organisms entrained from the thermocline (zooplankton, larval fish) may also be retained by the small-scale convergence zone at the shear front. Seabirds, including Cory's Shearwaters, may feed directly on the displaced organisms or on other consumers foraging at the site. The latter seems likely as Cory's Shearwaters feed mainly on actively swimming squid, crustaceans, and small fish (Clapp et al. 1982). Over half (56%) of the shearwaters observed on 13 July were sitting on the water surface, and many were submerging their heads or pecking at the surface.

Cory's Shearwaters are particularly dependent on features such as fronts that concentrate prey at the ocean surface. Unlike *Puffinus* shearwaters, *Calonectris* have long wings and weakly developed sterna, making them ill-suited for deep diving (Brown et al. 1978). Observations made on other dates (N = 55) and cruises (N = 13) in the South Atlantic Bight indicated that Cory's Shearwaters were most frequently encountered near the Gulf Stream front on the outer shelf. Shearwater abundance fell sharply when counts were continued either further offshore in the Gulf Stream or into

more inshore waters. Cory's Shearwaters also continued to associate with the front during the 10–30 km east–west meanders of the Gulf Stream that occur every 2–14 days (Lee and Brooks 1979, Lee and Atkinson, 1983).

Relationships between Cory's Shearwater distribution and water-mass boundaries (fronts) have been reported by Pulich (1982), who found that Cory's Shearwaters were associated with the 35–36‰ salinity boundary in the western Gulf of Mexico but found no relationship between the occurrence of shearwaters and surface temperatures. Pulich suggested that the front at the western Gulf continental shelf break may have attracted the shearwaters along with schools of tuna and mackerel. These results, along with our data showing extended seasonal association, suggest that fronts may be important foraging areas for post- and nonbreeding Cory's Shearwaters in the western North Atlantic.

SUMMARY

The abundance of Cory's Shearwaters (*Calonectris diomedea*) in the South Atlantic Bight in July and Oct. 1983 was correlated significantly with environmental changes associated with Gulf Stream surface thermal fronts. Density of the species within 4 km of the front was 14.9–37.7 birds/km² vs. 0.0–0.7 birds/km² elsewhere (≥4 km from the front). The average abundance (birds/transect) of Cory's Shearwaters on 13 July in near-front transects (<4 km) was significantly higher than in transects elsewhere ($P < 0.01$). The interactions of physical and biological processes that result in the association of Cory's Shearwaters with fronts are discussed.

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BROWN PELICAN POPULATIONS AND POLLUTANTS IN TEXAS 1975–1981

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Only a decade ago the population of Brown Pelicans (*Pelecanus occidentalis*) nesting in Texas was considered nonviable. From the mid-1950s through 1974 no more than 50 pelicans remained from a population that once numbered about 5000 individuals. During those years, there were few attempts at reproduction, and nesting pelicans seldom produced enough young to compensate for adult mortality. The history, status, and role of pesticides in the decline of this endangered species on the Gulf Coast from the early 1960s through 1974 was reviewed in an earlier paper (King et al. 1977). Our studies since 1974 indicate that reproductive success has improved and the population is increasing. The purpose of this paper is to present data gathered from 1975 through 1981 on environmental contaminants and to interpret contaminant influence on current Brown Pelican reproductive success and population status.

METHODS

We made year-round observations of known Brown Pelican habitats in coastal Texas to document numbers of nesting and wintering birds. Weekly observations were made throughout the nesting season from the onset of courtship through fledging. We observed the colonies from a distance of at least 200 m to minimize the effects of human disturbance. From 1975 through 1979, the nesting areas were not entered until most birds had been incubating for 2–3 weeks. In 1980 and 1981, we did not approach individual nests until young pelicans could be seen in most nests with the aid of binoculars. We then entered the colonies and examined unhatched eggs to assess viability. Abandoned eggs were collected for the analysis of contaminant residues and to measure shell thicknesses. Whole eggs were weighed and measured. The contents were removed, frozen, and stored in chemically cleaned jars.

Shell thicknesses of eggs collected from 1975 to 1981 were compared with those of museum eggs collected before the widespread use of DDT (pre-1947), and also, with measurements of eggs collected in 1970 reported by King et al. (1977). Only eggs from Texas colonies were used for comparisons of shell thickness. Because only addled eggs from abandoned nests were collected for residue analyses and measurements of shell thickness, our collection was not a random sample. Pollutant residues may have been biased towards higher levels, and shell-thickness values may have been lower than those obtained from a random collection of viable eggs.

Nestling pelicans were banded and color-marked just prior to fledging. Each pelican was banded with a Fish and Wildlife Service band on one leg and a rigid, colored, plastic band on the other leg. Colored bands were coded by year but not by the colony from which the young fledged.

During the study, two moribund pelicans were recovered from Corpus Christi Bay. Both pelicans died within 24 h of capture despite concerted efforts to keep them alive. The

birds were necropsied and brain and carcass tissues were saved for residue analyses. Pelican food items, including regurgitated fish, also were salvaged for residue analyses.

Analysis for chemical residues was conducted at the Patuxent Wildlife Research Center at Laurel, Maryland. Individual egg and tissue samples were analyzed for several organochlorine compounds based on methods described by Cromartie et al. (1975). Polychlorinated styrenes were quantified only in 1980 samples. The lower limit of quantification was 0.1 ppm for all organochlorine pesticides and 0.5 ppm for PCBs. The lower limit of quantification for residues in pelican food items collected from 1977 to 1979, was 0.1 ppm; samples from 1980 were analyzed to the nearest 0.01 ppm. All residues are expressed on a wet-weight basis.

Metal residues were quantified in samples collected from 1975 through 1978. Residues of arsenic, selenium, and zinc were measured under the standard conditions recommended by Perkin-Elmer, Norwalk, Conn. (1976). The lower detection limits of arsenic, selenium, and zinc were 0.05, 0.01, and 0.01 ppm, respectively. A 5-g sample for mercury analysis was digested by methods described by Monk (1961). Total mercury was determined by cold vapor atomic absorption spectrophotometry (Hatch and Ott 1968). The lower limit of reportable mercury residues was 0.02 ppm.

Statistical comparisons of residue levels and eggshell thicknesses were made using an analysis of variance. For samples in which no residues were detected, a value of one-half the lower detection limit was assigned and residues were then log–transformed for statistical tests. Residue levels were compared between years using Scheffe's Multiple Comparison procedure (Neter and Wasserman 1974). Spearman's Rank Correlations were calculated among residues and shell thickness values. Unless otherwise stated, a significance level of 0.05 was used.

RESULTS AND DISCUSSION

Population status.—Our observations, and reports incidental to other surveys (winter waterfowl survey, Audubon Christmas Bird Counts), indicated that fewer than 100 pelicans spent the winter months along the Texas Coast during 1970–1981. Wintering pelicans usually were concentrated in 2 areas; from 16 to 39 individuals were recorded on the central coast in the San Antonio–Corpus Christi Bay areas, and up to 40 individuals were recorded in the Lower Laguna Madre near Port Isabel (Fig. 1). Infrequent sightings of 1 to 3 pelicans were made in the Freeport–Galveston Bay area. Most pelicans wintering on the central coast were adults, whereas most observed near Port Isabel were subadults.

Each year, pelican numbers increased slowly during the spring and summer months and peaked in Aug. or Sept. The maximum number of pelicans seen annually varied from 90 individuals in 1975 to about 500 individuals in 1979 (Table 1). Most of the pelicans observed during late summer were unbanded subadults. Because almost all nestling pelicans from Texas and Louisiana were banded before they fledged, we suspect that the large influx of unbanded subadults were pelicans from Mexican colonies.

Nesting populations.—The number of pelicans nesting in Texas increased from 18 pairs in 1975 to 57 in 1981 (Table 1). Pelicans established

TABLE 1
BROWN PELICAN POPULATIONS AND REPRODUCTIVE PERFORMANCE IN TEXAS, 1975–1981

Year	Estimated number			Maximum number of individuals[a]
	Nesting pairs	Young fledged	Young per pair	
1975	18	9	0.5	90
1976	16	16	1.0	90
1977	17	34	2.0	112
1978	23–25[b]	37[c]	1.5–1.6	350
1979	33–38[b]	46[d]	1.2–1.4	500
1980	40–54[b]	76	1.4–1.9	400–450
1981	57	46	0.8	430–470

[a] Includes nesting pelicans, fledged young, and immigrants. Peak populations were recorded in July or Aug. each year.
[b] Nest abandonment and possible renesting made more precise counts impossible.
[c] Thirty-eight young reached fledging size but one was blind in one eye and was collected for a zoo.
[d] One tame juvenile pelican was reported at several locations on the central coast. After several unsuccessful attempts to integrate the bird into the wild population, it was placed in a zoo.

colonies at eight locations along the coastal bend between Aransas and Corpus Christi bays (Fig. 1). They nested on 5 islands in the San Antonio–Aransas Bay area: North, Carroll, Deadman, False Live Oak Point, and Long Reef. In Corpus Christi Bay, they nested only on Pelican Island. For the first time since the population crash in the late 1950s, Brown Pelicans nested on the upper Texas coast in 1980 and 1981. A lone pair built a nest both years on a small dredge-material island in Cedar Lakes within the boundaries of San Bernard National Wildlife Refuge.

Nesting activities frequently began 2–3 weeks earlier at the Aransas Bay area than at Pelican Island in Corpus Christi Bay. Courtship and nest site selection at Aransas Bay usually were initiated in mid- to late Feb. with most birds incubating by mid–March. Nesting activities were more synchronized at Aransas Bay than at Pelican Island. Most pairs were incubating by late March at Pelican Island, but a few late nesting birds were still incubating eggs in late June. Although renesting of Brown Pelicans has been documented by Schreiber (1979), we were unable to determine if pelicans that abandoned their nests at Aransas Bay renested at Corpus Christi Bay.

Reproductive success.—Average clutch size varied from 2.0 (N = 18) in 1975 to 3.25 (N = 16) in 1976. Estimates of fledging success varied from 0.5 in 1975 to 2.0 in 1977 (Table 1) and probably were low because we were unable to document renesting attempts. Henny (1972) calculated that recruitment necessary to maintain a stable population was between 1.2 and 1.5 young per pair. Schreiber (1979) discussed recruitment in detail, and his data suggested that normal nesting success was close to, or

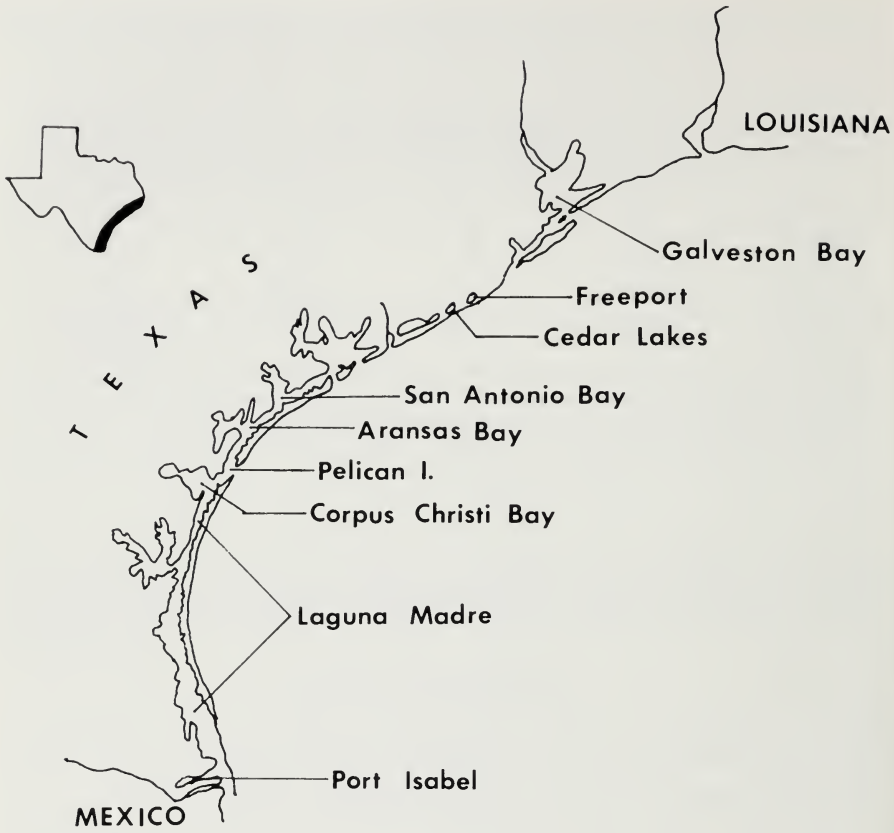

FIG. 1. Locations of Brown Pelican colonies and wintering areas on the Texas Coast.

slightly below, one young fledged per pair per year. By either estimate, recruitment in Texas colonies was adequate during all years, except perhaps in 1975.

Reproduction in terms of total young produced has improved greatly in recent years. For example, in the 11-year period from 1964 to 1974, only 46 pelicans were fledged from Texas colonies (King et al. 1977). In contrast, more than five times as many young (264) were fledged between 1975 and 1981.

Sighting rates of color-banded fledgling pelicans observed on and near the colonies in subsequent nesting seasons indicate that many subadult Texas pelicans do not return to nesting sites during the first breeding season following fledging (Table 2). Greater numbers of each year's cohort usually were observed in the second and third year after fledging. This

TABLE 2

RESIGHTING RATES[a] OF TEXAS COLOR-BANDED BROWN PELICANS COMPARED WITH THOSE IN SOUTH CAROLINA AND CALIFORNIA

Age class	Estimated % survival[b]		
	Texas	South Carolina	California
1st-year	22	40	50
2nd-year	27	30	37
3rd-year	23	25	32
4th-year	19	20	27

[a] Resighting rate = % of total young banded that were observed in each following year.

[b] Texas = this study; data indicate that many 1st- and 2nd-year pelicans do not return to their breeding areas in the subsequent nesting season. South Carolina = data based on Henny's (1972) mortality estimates adjusted for band loss. California = Anderson and Gress (1983), hypothetical survival rates.

phenomenon precludes accurate estimates of survival through the first and second year. Pelican survival to the third and fourth year, however, are in close agreement with estimates of survival rates for South Carolina and California populations (Henny 1972, Anderson and Gress 1983).

Organochlorine residues.—From 2 to 57 addled eggs were salvaged each year for residue analyses and eggshell thickness comparisons. DDT and its metabolites, primarly DDE, were detected in all eggs and geometric mean levels of DDE varied from 0.9 to 2.3 ppm annually (Appendix 1) and were lowest in 1976 and 1979. There has been a decline in DDE residues over the past decade with levels observed in the 1975–81 samples about one-half those (3.2 ppm) reported by King et al. (1977) for eggs collected in 1970.

Although DDE in Texas pelican eggs declined from 1970 to 1975–81, mean residues remained higher than those reported most recently in eggs from South Carolina and Louisiana. Average DDE residues in South Carolina eggs declined from 5.4 ppm in 1969 to about 0.8 ppm in 1977 (Blus et al. 1979b, Mendenhall and Prouty 1979), then showed little change through 1980 (Patuxent Wildlife Research Center, unpublished data). In Louisiana, declining DDE residues also leveled off at less than 1.0 ppm between 1974 and 1976 (Blus et al. 1979a).

Current levels of DDE apparently pose a minimal threat to pelican reproduction. The parent compound, DDT, was confirmed in one or more eggs each year except 1977, indicating recent exposure to the compound. With the exception of slightly elevated DDE levels found in the small sample of eggs collected in 1977 and 1978, the residues in our samples were similar to the 1.67 ppm reported by Schreiber and Risebrough (1972) for eggs in stable Florida populations. The maximum DDE residue in

pelican eggs from successful South Carolina nests was 3.7 ppm, and egg residue levels that exceeded 3.0 ppm were associated with substantially impaired reproductive success (Blus 1982). About 7% of the eggs in our collection contained DDE residues that approached the 3.0 ppm critical level. In contrast, more than 70% of the eggs collected in 1970 had 3.0 ppm or more DDE (King et al. 1977).

Dieldrin residues were detected in all eggs collected from 1975 through 1978. Residues averaged 0.3 ppm or less in all years and were below levels reported in pelican eggs from South Carolina, Florida, and Louisiana (Blus et al. 1977, 1979a, b). The critical level of dieldrin in pelican eggs associated with impaired reproductive success exceeds one ppm (Blus 1982). Current levels of dieldrin in Texas pelicans apparently do not pose a threat to reproductive success and survival.

Other organochlorine insecticides including chlordane-related compounds, HCB, and toxaphene were infrequently detected, usually at <1.0 ppm, and were not considered biologically significant. Endrin was recovered in pelican eggs only in 1975 when 15 of 18 eggs contained from 0.1 to 0.3 ppm. The presence of endrin in 1975 is of special interest because endrin in Louisiana pelican eggs also peaked that year and maximum residues coincided with a die-off in 1975 of large numbers of White (*Pelecanus erythrorhynchos*) and Brown pelicans in Louisiana (Nesbitt et al. 1978, Blus et al. 1979a).

PCBs, like DDE, were recovered in all eggs with one exception (Appendix 1). Residues in 1976 samples were lower than those of other years. PCB concentrations that averaged 9.37 ppm in 1970 (King et al. 1977) declined more than eight-fold by 1981. The decline in PCB residues in Texas Brown Pelican eggs is in notable contrast to the relatively stable levels reported in pelican eggs from South Carolina and Louisiana (Mendenhall and Prouty 1979, Blus et al. 1979a).

During the course of this study, 2 adult female pelicans were found moribund, and brain and carcass samples were salvaged for residue analyses. Lethal residues of DDT plus DDD in the brain generally exceed 20–30 ppm (Bernard 1963, Stickel et al. 1966, Hill et al. 1971). DDT residues in the brain tissues of our pelican samples were 1.1 and 0.5 ppm; therefore, death was not a result of DDT poisoning. No other organochlorine insecticide residues were detected in the brain. One sample contained low (1.0 ppm) residues of PCB. Although brain residues were relatively low, DDT carcass levels (14 and 26 ppm) were higher than those reported by Blus et al. (1977) in tissues of four Georgia and Florida pelicans found dead ($\bar{x} = 5.4$, range = 0.9–13.0 ppm).

Organochlorine residues were not detected in the 19 pelican food items (regurgitated fish; *Brevoortia patronus* and *Anchoa mitchilli*) collected

between 1977 and 1979 that were analyzed to the nearest 0.1 ppm. Eleven of 12 Gulf Menhaden (*B. patronus*) collected in 1980 and analyzed to the nearest 0.01 ppm contained an average of 0.06 ppm DDE. There was no difference in DDE levels between the Carroll Island and Pelican Island samples. In addition to DDE and DDD, one sample from Carroll Island also contained 0.03 ppm DDT. Low levels (<0.04 ppm) of chlordane, HCB, dieldrin, and octachlorostyrene were found in fewer than one-half of the fish. PCB was detected in 6 of 12 samples at <0.25 ppm.

Both DDE and DDT were detected in fish and in pelican eggs collected in 1980. DDT and metabolite residues may have been magnified 23 times from fish (0.06 ppm) to pelican eggs (1.36 ppm), but interpretation of this apparent biomagnification is complicated by the migratory habits of the pelicans and their prey.

As the use of DDT was suspended in 1972, we found it of interest that pelican food items contained both DDD and DDT in addition to DDE. The presence of DDT suggested that the fish were recently exposed to that compound. In the past, we hypothesized that Brown Pelicans nesting in Texas acquired most of their DDE burdens on wintering areas in Mexico. Because DDT was recovered in food fish from Texas waters, contamination from local sources was apparent.

Metal and selenium residues.—Mercury, arsenic, and selenium residues in Texas pelican eggs averaged 0.5 ppm or less (Appendix 2). Mercury ranged from 0.04 to 0.60 ppm and was recovered in all eggs. Residues were generally below levels associated with decreased hatchability and nestling survival of other species of birds (Fimreite 1971, Spann et al. 1972, Vermeer et al. 1973, Connors et al. 1975, Heinz 1976). From 1974 to 1978, mean mercury levels in Texas pelican eggs (0.04–0.28 ppm) were similar to, or lower than, those reported in pelican eggs collected from South Carolina and Florida (Blus et al. 1977). In contrast, mercury values were slightly greater in Texas pelican eggs than levels in Louisiana eggs (Blus et al. 1975). Mercury residues below 0.25 ppm in eggs of some species may represent background levels (Faber and Hickey 1973). About 73% of the eggs in our sample contained mercury residues below 0.25 ppm.

Mean selenium residues varied from 0.21 to 0.50 ppm and were 1.3 to 3.6 times greater than those in South Carolina and Florida eggs (Blus et al. 1977). The toxicity of selenium at the maximum level found in this study, 0.65 ppm, has not been determined. Selenium residues in the eggs of healthy chickens maintained on an adequate diet averaged about 0.30 ppm (Latshaw 1975). The maximum arsenic residue found in Texas pelican eggs was 0.26 ppm, slightly below the mean level (0.31 ppm) in South Carolina eggs but greater than average levels (0.10 ppm) in eggs from

Florida colonies (Blus et al. 1977). Levels of zinc were below those found in eggs from a stable Common Tern (*Sterna hirundo*) colony on Great Gull Island, New York (Connors et al. 1975). The residue levels of arsenic and zinc were low and probably represent background levels that had little effect on pelican reproduction or survival.

Most insecticide residues were positively associated with each other and with PCB levels (Appendix 3). The only significant association between metal residues was a positive relation between arsenic and selenium.

Oil pollution.—Because of their gregarious behavior, feeding habits, and preference for shallow coastal waters, pelicans are highly vulnerable to oil pollution (Clapp et al. 1982). Despite the relatively small number of pelicans in Texas, there have been numerous observations of oiled birds. The 3 June 1979 blowout and resultant spill from the Ixtoc I oil well in the Bay of Campeche, Mexico, caused considerable concern for the welfare of Brown Pelicans in Mexico and Texas. Although pelicans occasionally were seen outside the barrier islands, their primary nesting, feeding, and loafing areas were within the various bay systems. Booms kept most of the oil from entering Corpus Christi and Aransas bays. Despite these preventive measures, 8 Brown Pelicans were observed with oil on their feathers, but no pelicans were found completely debilitated by oil. In another incident, a pipeline rupture in Oct. 1976 resulted in the fatal oiling of one adult pelican (King et al. 1979).

Eggshell thinning.—Annual mean shell thickness of eggs analyzed for pollutant residues varied from 0.48 to 0.54 mm, about 4–14% thinner than normal (Table 3). The mean shell thickness of eggs collected from 1975 to 1981 was no different than that reported by King et al. (1977) for eggshells collected in 1970, but current thickness remained significantly ($P < 0.01$) less than that of eggs collected before the wide-spread use of DDT (pre-1947). An inverse correlation between eggshell thickness and DDE and PCB residues was reported in 1970 samples (King et al. 1977); however, only a weak correlation ($P < 0.06$) was found between shell thickness and DDE residues in eggs collected from 1975 to 1981 (Appendix 3).

SUMMARY

The population status, reproductive success, and levels of environmental contaminants in Brown Pelicans (*Pelecanus occidentalis*) in Texas were studied from 1975 through 1981. Breeding populations increased from 18 pairs in 1975 to 57 pairs in 1981. All unhatched eggs salvaged for analyses of contaminant residues contained DDT metabolites. Mean DDE levels varied from 0.9 to 2.4 ppm and about 7% of the samples had residues that approached critical levels that could affect reproductive success. DDE levels did not decline from 1975 to 1981 and residues leveled off at higher values than those in South Carolina and Louisiana pelican populations. PCB residues also remained stable. Endrin was detected only in 1975,

TABLE 3
SHELL MEASUREMENTS OF TEXAS BROWN PELICAN EGGS

Collection date (N)	Mean thickness (range) mm	% change from pre-1947 value
Pre-1947 (43)[a]	0.56 (NA)[b]	—
1970 (14)	0.50 (0.41–0.60)	−11
1975 (18)	0.50 (0.44–0.55)	−11
1976 (9)	0.52 (0.50–0.59)	−7
1977 (2)	0.54 (0.53–0.55)	−4
1978 (4)	0.48 (0.41–0.52)	−14
1979 (9)	0.48 (0.44–0.53)	−14
1980 (4)	0.53 (0.46–0.61)	−5
1981 (57)	0.51 (0.44–0.59)	−9

[a] N = number of eggs measured. Pre-1947 data from Anderson and Hickey (1970), 1970 data from King et al. (1977).
[b] NA = data not available.

and paralleled peak levels in Louisiana pelican eggs and coincided with the 1975 endrin-caused die-off of White and Brown pelicans in Louisiana. Residues of mercury, arsenic, selenium, and zinc were low and probably had little effect on pelican reproduction and survival. Mean eggshell thickness was 4–14% thinner than normal, but we found no evidence that shell thinning adversely affected reproduction. Observations of color-marked young indicated that not all one- and two-year-old pelicans returned to Texas nesting areas. Subadult survival through the third and fourth year was similar to survival rates of South Carolina and California Brown Pelicans. Overall reproductive success improved and the population is increasing.

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Appendix 1

Organochlorine Residues in Texas Brown Pelican Eggs, 1975–1981

Year	No. eggs	Geometric mean residue ppm wet weight, (N), 95% confidence interval, and range[a]					
		DDE	DDD	DDT	Dieldrin	Chlordane[b]	PCB
1975	18	1.7 (18)A[c]	0.3 (18)AB	— (4)	0.3 (18)A	0.2 (16)A	4.0 (18)A
		1.4–2.0	0.2–0.3	—	0.3–0.4	—	3.4–4.6
		0.9–3.0	0.1–0.7	0.1–0.2	0.2–0.5	0.1–0.6	2.4–7.3
1976	9	0.9 (9)B	0.1 (8)B	— (2)	0.2 (9)AB	— (1)	0.8 (9)B
		0.7–1.1	0.1–0.2	—	0.1–0.3	—	0.4–1.6
		0.6–1.8	0.1–0.4	0.1–0.2	0.1–0.4	0.1	1.0–1.6
1977	2	2.3 (2)A	0.7 (2)A	— (1)	0.1 (2)B	ND	2.8 (2)A
		0.8–6.9	0.0–373	—	0.0–0.3		1.5–5.6
		2.3–2.6	0.4–1.2	0.8	0.1		3.0–2.7
1978	4	2.2 (4)A	0.2 (4)AB	— (1)	0.1 (4)AB	0.2 (4)A	3.5 (4)A
		1.7–2.9	0.1–0.4	—	0.1–0.2	—	2.4–5.0
		0.4–2.5	0.2–0.4	0.1	0.1–0.2	0.1–0.4	2.5–4.0
1979	9	0.9 (9)B	— (2)	— (1)	0.1 (4)B	— (2)	1.4 (9)A
		0.5–1.4	—	—	0.0–0.1	—	0.9–2.2
		0.4–2.5	0.1–0.4	0.1	0.1–0.2	0.1–0.2	0.6–2.5
1980	4	1.4 (4)A	0.1 (3)B	— (1)	0.1 (2)B	— (1)	1.8 (4)A
		0.8–2.4	0.0–0.5	—	0.0–0.2	—	1.4–2.3
		1.0–2.2	0.1–0.3	0.1	0.1–0.2	0.1	1.6–2.2
1981	57	1.3 (57)A	0.2 (48)B	— (2)	0.1 (34)B	— (15)	1.1 (56)A
		1.2–1.4	0.1–0.2	—	0.0–0.1	—	1.0–1.3
		0.5–2.5	0.1–0.8	0.2	0.1–0.3	0.1–0.5	0.6–2.8

[a] Dashes indicate that the frequency of detection was <50% and the mean was not calculated. (N) = number of samples with detectable residues. ND = No residue detected. Range = high and low extremes of detected residues. HCB was detected in 18 eggs in 1975, mean = 0.08 (0.1–0.2 ppm). Heptachlor epoxide was recovered in 6 eggs in 1975, mean = 0.15 (0.1–0.2 ppm). Endrin was found in 15 of 18 eggs in 1975, mean = 0.15 (0.1–0.3 ppm). Toxaphene was observed in 3 eggs in 1975 (0.2, 0.5, 0.5 ppm) and in one egg in 1976, 0.07 ppm.

[b] Total chlordane isomers = *cis*-chlordane + *trans*-nonachlor + *cis*-nonachlor. Samples collected in 1979 were not analyzed for *trans*-nonachlor.

[c] Means sharing the same letter suffix are not significantly different from each other.

Appendix 2

Metal and Selenium Residues in Texas Brown Pelican Eggs

Year	No. eggs	Geometric mean residue, (95% CI), and range[a]			
		Arsenic	Mercury	Selenium	Zinc
1975	18	0.10A (0.09–0.12) 0.07–0.25	0.16A (0.11–0.23) 0.07–0.54	0.45A (0.41–0.49) 0.13–0.57	NA
1976	9	0.09A (0.07–0.12) 0.05–0.14	0.11A (0.07–0.17) 0.07–0.46	0.50A (0.43–0.57) 0.37–0.65	8.82A (8.16–9.52) 7.60–10.40
1977	2	0.25B (0.20–0.33) 0.25–0.26	0.04B (0.01–0.18) 0.04–0.05	0.43A (0.01–18.8) 0.32–0.58	4.93A (0.63–38.4) 4.20–5.80
1978	4[b]	0.03 (0.02–0.07) 0.06	0.28C (0.12–0.65) 0.18–0.60	0.21B (0.13–0.33) 0.15–0.29	6.90A (3.75–12.7) 4.60–10.0

[a] Residues expressed in ppm wet weight. NA = not analyzed. Numbers in parentheses indicate 95% confidence intervals. Means sharing the same letter suffix are not significantly different from each other.

[b] Only 1 of 4 eggs contained a detectable residue.

Appendix 3

Intercorrelation of Major Contaminant Residues and Shell Thickness of Texas Brown Pelican Eggs

		DDE	DDD	Dieldrin	PCB	AS	HG	SE	ZN
DDE	r[a]	1.00000	0.49600	0.33617	0.67600	−0.08991	0.40149	−0.40406	−0.22898
	P	0.0000	0.0001	0.0005	0.0001	0.6188	0.0206	0.0197	0.4117
	N	114	114	103	114	33	33	33	15
DDD	*r*	0.49600	1.00000	0.41751	0.18039	0.09178	0.36487	−0.07536	−0.46307
	P	0.0001	0.0000	0.0001	0.0548	0.6114	0.0368	0.6768	0.0822
	N	114	114	103	114	33	33	33	15
Dieldrin	*r*	0.33617	0.41751	1.00000	0.48995	−0.04758	−0.06984	0.00595	0.44425
	P	0.0005	0.0001	0.0000	0.0001	0.7926	0.6994	0.9738	0.0971
	N	103	103	103	103	33	33	33	15
PCB	*r*	0.67600	0.18039	0.48995	1.00000	−0.04600	0.01759	−0.34896	−0.24798
	P	0.0001	0.0548	0.0001	0.0000	0.7993	0.9226	0.0465	0.3729
	N	114	114	103	114	33	33	33	15
AS	*r*	−0.08991	0.09178	−0.04758	−0.04600	1.00000	−0.29143	0.42442	−0.23001
	P	0.6188	0.6114	0.7926	0.7993	0.0000	0.0999	0.0138	0.4096
	N	33	33	33	33	33	33	33	15
HG	*r*	0.40149	0.36487	−0.06984	0.01759	−0.29143	1.00000	−0.10692	0.26834
	P	0.0206	0.0368	0.6994	0.9226	0.0999	0.0000	0.5537	0.3335
	N	33	33	33	33	33	33	33	15
SE	*r*	−0.40406	−0.07536	0.00595	−0.34896	0.42442	−0.10692	1.00000	0.25873
	P	0.0197	0.6768	0.9738	0.0465	0.0138	0.5537	0.0000	0.3518
	N	33	33	33	33	33	33	33	15
ZN	*r*	−0.22898	−0.46307	0.44425	−0.24798	−0.23001	0.26834	0.25873	1.00000
	P	0.4117	0.0822	0.0971	0.3729	0.4096	0.3335	0.3518	0.0000
	N	15	15	15	15	15	15	15	15
THICK	*r*	−0.17605	−0.10805	−0.13739	−0.13875	0.02121	−0.26228	−0.01041	0.02693
	P	0.0610	0.2525	0.1664	0.1410	0.9067	0.1403	0.9542	0.9241
	N	114	114	103	114	33	33	33	15

GENERAL NOTES

Wilson Bull., 97(2), 1985, pp. 215–219

Home range and habitat use of forest-dwelling Mallards in Minnesota.—Estimates of home range size for radio-equipped female Mallards (*Anas platyrhynchos*) vary from 468 ha in North Dakota (Dwyer et al., J. Wildl. Manage. 43:526–531, 1979) to 210 ha in forested north-central Minnesota (Gilmer et al., J. Wildl. Manage. 39:781–789, 1975). Although the North Dakota study was of rather typical Mallard habitat, albeit with a relatively low density of the species, the Minnesota study was of birds that principally used small wetlands. A range of response by Mallards to the quantity, quality, and spatial arrangement of breeding habitat is thus suggested. This paper provides further data obtained from a sample of birds that used primarily rivers and large (>2500 ha) sand-lake complexes adjacent to the study area discussed by Gilmer et al. (1975).

Study area and methods.—The 39-km² study area was 18 km east of Bemidji, Beltrami Co., Minnesota, along the Mississippi River at the western boundary of the Chippewa National Forest. Six wetland complexes (Cowardin and Johnson, U.S. Fish Wildl. Serv. Spec. Sci. Rept. Wildl. 168, 1973), were present: sand lakes, river marsh, river channel, intermediate lakes, bog lakes, and nonpermanent wetlands. Nonpermanent wetlands >100 m from a lake or river shoreline were designated as interior wetlands; those <100 m were considered adjacent wetlands. Total area of interior nonpermanent wetlands was 38.6 ha. Adjacent wetlands averaged 0.6 ha and occurred at a density of one wetland per 1.6 km of shoreline. Shoreline lengths were 21.7 km for sand lakes and 5.1 km for river channels. Thirty-seven percent of the shoreline was bounded by a mat of floating vegetation consisting primarily of sedges (*Carex lasiocarpa, C. aquatilis, C. lacustris*), bluejoint reedgrass (*Calamagrostis canadensis*), willows (*Salix* spp.), and mountain alder (*Alnus incana*). Other shorelines were bounded by sand and rock beaches, overhanging upland brush, and residential development. River marsh areas constituted 62.0 ha, consisting primarily of floating mat vegetation, as above, and emergent stands of common reed (*Phragmites communis*) and cattail (*Typha* spp.).

In early spring 1971 and 1972, birds were captured by nightlighting from an airboat or with small recoilless rocket nets, and were equipped with radio transmitters (Gilmer et al., J. Wildl. Manage. 38:243–252, 1974) and fitted with Fish and Wildlife Service leg bands. Techniques for locating radio-equipped birds in this area were summarized by Gilmer et al. (J. Wildl. Manage. 41:345–359, 1977). Locations were keyed to habitat by the use of digitized maps (Gilmer et al., J. Wildl. Manage. 37:404–409, 1973); field maps were either photographs with a coordinate grid or vegetation maps made from the photographs and ground survey. Habitat types were those identified by Cowardin and Johnson (1973). To permit comparison with earlier studies, maximum home ranges were delineated by connecting the outermost telemetry locations obtained during the entire breeding season to form a polygon (Odum and Kuenzler, Auk 72:128–137, 1955). Habitat use was calculated as the percentage of total locations, but did not include locations of a bird on a nest. Available habitat was considered only to be that contained within a bird's home range and did not include open water. To reduce bias attributable to inadequate sampling of bird activities, we conservatively selected for home range analysis only those birds for which we had >100 locations recorded over ≥30 days of tracking history, and for which one or more nest attempts were recorded. These restrictions left 13 Mallards (5 marked pairs plus 3 females) having a mean tracking rate of 7.2 locations per day per bird for analysis of home range size.

TABLE 1

VARIATIONS IN HOME RANGE OF FIVE MALLARD FEMALES FOLLOWING NEST DESTRUCTION

Female	1st nesting period			Renesting interval[a]		2nd nesting period			Overall	
	Home range (ha)	Days	Stage destroyed	Home range (ha)	Days	Home range (ha)	Days	Distance between renests (m)	Home range (ha)	Tracking period
5147	3.7	5	Early incubation	7.4	12	13.2	12	547.1	76.0	4/29–6/2
5200[b]	97.4	15	Early incubation	63.2	6	257.8	37	3203.2	997.7	4/19–7/9
5222	82.0	19	Late incubation	114.3	19	5.8	18	1340.8	223.0	5/17–7/12
5256	6.2	8	Late incubation	18.0	9	27.2	29	82.0	32.6	4/29–6/13
5259	92.5	10	Early incubation	181.0	17	111.9	23	1443.0	389.6	5/6–6/24

[a] As defined by Sowls (Prairie Ducks, The Stackpole Co., Harrisburg, Pennsylvania, and Wildlife Management Institute, Washington, DC, 1955): the period between destruction of one nest and the laying of the first egg in the next.

[b] Tracked for 11 days prior to her first nest attempt—home range size for this prenesting period was 950 ha (95% of her total breeding home range).

Two females primarily used residential shoreline/marine areas and stands of vegetation in river mouths. As this habitat was available only in the areas used by these birds, we deleted these 2 birds from comparison of habitat use throughout the study area. Four of the six remaining females shifted from using the river channel (the first open water) to using the river marsh or sand lake as the season progressed. Habitat-use data for these birds were therefore analyzed separately for early and late portions of the year; 10 analyses of habitat use by females were then possible. Because of the limitations imposed by the restriction of analysis to only those birds for which we had substantial data, we used Wilcoxon's matched-

TABLE 2

MEAN AVAILABILITY (% OF TOTAL WETLAND AREA LESS OPEN WATER) AND USE (% OF TOTAL RADIO LOCATIONS) OF 9 WETLAND TYPES IN 10 HOME RANGES OF FEMALE MALLARDS IN NORTH-CENTRAL MINNESOTA 1971 AND 1972

Wetland type[a]	Availability	Use	Preference[b]
Interior nonpermanent wetlands	13.95	2.73	R
Adjacent nonpermanent wetlands	6.77	7.68	NS
Phragmites communis	6.24	7.93	NS
Typha spp.	14.85	14.16	NS
Deep/shallow marsh	4.74	7.88	P
Bog mats	21.25	32.28	P
Overhanging brush	8.92	8.41	NS
Composite lake shoreline	24.29	25.52	NS
Emergent aquatics/bog mat	7.66	1.66	R

[a] Habitat types from Cowardin and Johnson (1973).

[b] Based on the difference between observed and expected use of the types according to their availability in the home range. Preference (P) or rejection (R) indicate significance ($P < 0.10$); NS = nonsignificant.

TABLE 3

MEAN AVAILABILITY (%) AND USE (%) OF WETLAND COMPLEXES BY MALLARD PAIRS GROUPED BY HOME RANGE SIZE AND USE OF RIVER HABITAT ON THE NORTH-CENTRAL MINNESOTA STUDY AREA, APRIL–JUNE 1971 AND 1972

	Mean home-range size					
	53 ha[a] (N = 3)		347 ha[b] (N = 4)		871 ha[c] (N = 3)	
Wetland	Available	Used	Available	Used	Available	Used
Nonpermanent wetlands	5	<1	17	9	33	16
Bog lakes	0	0	0	0	2	2
Intermediate lakes	0	0	6	8	2	2
Sand lakes	12	3	20	8	42	66
River channel	20	35	20	57	8	5
River marsh	63	62	37	18	13	9

[a] 32.6, 49.0, and 75.9 ha.
[b] 147.5, 302.0, 392.6, and 549.2 ha.
[c] 768.7, 851.9, and 988.7 ha.

pairs signed-rank test (Wilcoxon, Biometrics Bull. 1:80–83, 1945), a nonparametric analogue to the paired-sample *t*-test, to test for preference or rejection of various habitats.

Results and discussion.—Mean home range size was 540 ha (40–1440 ha) for eight female Mallards and 620 ha (70–1140 ha) for five males. Five home ranges of individual birds were less than 100 ha and six exceeded 750 ha. The extreme variability in home range sizes and the scarcity of intermediate values contrasted markedly with the data obtained from Mallards using interior wetlands in an adjoining area (Gilmer et al. 1975). In that study, home range size averaged 210 ha for females and 240 ha for males and only one pair had a home range in excess of 750 ha.

We found it difficult to assess within-season mobility of the female Mallards because they were captured during different portions of the nesting cycle, and substantial nest destruction occurred. Differential mobility of females during various portions of the nesting cycle (generally reduced from nest site selection through incubation) has been documented by several authors (Dzubin, Trans. N. Am. Wildl. Conf. 20:278–298, 1955; Gates, Wilson Bull. 74:43–67, 1962; Derrickson, Auk 95:104–114, 1978; Titman, Can. J. Zool. 61:839–847, 1983), but less is known of changes between individual nesting attempts by the same bird. We obtained enough data to analyze five renesting attempts (Table 1). Four of the five females used larger areas between nesting attempts than during the nesting periods, and larger areas during the second than the first nesting interval, but the latter may have been an artifact of the truncation of the first nesting cycle. Renesting thus certainly had a positive effect upon home range size of the female, unlike the conclusion reached by Derrickson (1978:109) from review of the literature and study of Northern Pintails (*Anas acuta*) in North Dakota.

Wilcoxon's matched-pairs signed-rank test indicated preference and rejection of four of the wetland types at a low level of significance (Table 2). We interpreted these data to indicate a preference for undisturbed shorelines with emergent vegetation and overhanging brush, which provided isolation and concealment, and of bog mat shorelines, which provided similar resources and numerous loafing sites. All birds frequented areas with substantial interspersion of physical and floral features and spent little time along sparsely vegetated shorelines. Overhanging brush attracted many birds even in the absence of emergent vege-

tation in the adjacent water. *Phragmites communis,* a vegetation type not usually associated with substantial use by Mallard pairs, provided roosting and loafing cover and isolation for the birds. The shoreline types used most by Mallards in our study were those used most by Mallards in adjacent areas (Gilmer et al. 1975). The major difference between the birds in the two areas was the fact that nonpermanent wetlands were not used by the birds initially captured on sand lakes and on river marshes.

Birds with small and intermediate home ranges had consistently high use of river marsh and river channels (Table 3), and home range size was negatively correlated with percent use of river habitat ($r = -0.929$, $P < 0.01$). River–marsh areas were preferred for night roosting by birds in all three categories of home range size, as is shown by the differences in percent of day vs night use of this habitat: small home range—day 63% and night 67%, medium home range—day 14% and night 83%, large home range—day 6% and night 40%. During spring nightlighting operations near the peak of nesting activities, we found as many as seven Mallard pairs along a densely vegetated 50-m river channel. This sharing of habitat during certain periods differs from the behavior of the obligatory river-dwelling African Black Duck (*Anas sparsa*), which demonstrates no home range overlap and maintains a strict defense of territory boundaries (Ball et al., Wildfowl 29:61–79, 1978; McKinney et al., Z. Tierpsychol. 48:349–400, 1978). The African Black Duck defends a small exclusive territory; the Mallard in Minnesota uses large areas that overlap with the areas of other pairs. Separation of Mallard pairs was nevertheless accomplished in time and space; we observed few encounters between pairs. The ability of birds to join loose flocks at night has obvious survival advantages in an area with numerous predators and few appropriate roosting sites.

The need for seclusion and isolation by Mallard pairs, and the species' intolerance and avoidance of conspecifics during the breeding period have been emphasized by several authors (Barclay, Ph.D. diss., Ohio State Univ., Columbus, Ohio, 1970; Dzubin, Can. Wildl. Rept. Ser. 6:138–160, 1969; McKinney, Wildfowl Trust Ann Rept. 16:92–106, 1965; Titman 1983; and others). As expected, more than 50% of the daytime locations of pairs with large home ranges were in habitats, such as sand bars and rock beaches, where birds were fairly visible and were separated by great distances from conspecifics. Almost 90% of the locations of pairs with small home ranges, but only 17% of the locations of pairs with large home ranges were in communities providing the most cover, such as cattails, bog mat shorelines, and overhanging brush shorelines. Pairs with intermediate-size home ranges were found in high-concealment communities 60% of the time.

Dwyer et al. (1979) concluded that major differences in type and distribution of water areas are reflected in home range size differences between Mallards on the prairies and in forested areas. Results of our study suggest that similar relationships exist within forested regions. The ability of pairs to share certain parts of their home ranges and to respond quickly to various local conditions (McKinney 1965:104) is adaptive for Mallards in north-central Minnesota.

We have documented a wider range of home range sizes than heretofore indicated for Mallards in forested areas. This suggests a continuum of response by Mallards to the set of habitat conditions engendered by wetlands of varying quality and distribution, a conclusion reached by Nudds and Ankney for dabbling ducks generally (Wildfowl 33:58–62, 1982). The need for site-specific assessments of Mallard behavior and habitat use, as well as further studies of Mallards in forested habitat, is apparent.

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on statistical methodology, D. A. Davenport assisted with data processing, and the Cedar Creek Bioelectronics Laboratory of the Univ. Minnesota constructed and maintained our biotelemetry equipment. We especially thank our coworkers I. J. Ball and D. S. Gilmer for advice regarding conduct of this study and for comments on early drafts of the manuscript. W. H. Dryer, D. H. Johnson, J. T. Lokemoen, R. D. Titman, and an anonymous referee provided additional manuscript review.—Ronald E. Kirby and John H. Riechmann, *Dept. Ecology and Behavioral Biology, Univ. Minnesota, Minneapolis, Minnesota 55455*; and Lewis M. Cowardin, *U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, Jamestown, North Dakota 58401.* (Present address of REK: *U.S. Fish and Wildlife Service, Office of Information Transfer, 2629 Redwing Rd., Ft. Collins, Colorado 80526;* present address of JHR: *RR #2, Box 163, Valmeyer, Illinois 62295.* Address reprint requests to LMC.) *Accepted 10 Jan. 1985.*

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Observations of the formation of a Sage Grouse lek.—Sage Grouse (*Centrocercus urophasianus*) commonly use disturbed areas as breeding arenas (Dalke et al., J. Wildl. Manage. 27:811–840, 1963; Connelly et al., J. Range Manage. 34:153–154, 1981); however, few data are available on the establishment of leks by Sage Grouse. During a study of Sage Grouse use of a prescribed burn site, observations of three wing-tagged male and three radio-collared female grouse on a recently burned area provided some insight into the establishment of an arena.

My study was conducted on a 300 km^2 segment of the Idaho National Engineering Laboratory (INEL) in southeast Idaho. The area surrounding the burn site is dominated by big sagebrush (*Artemisia tridentata*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and perennial grasses (mostly *Pseudoroegnaria spicata* and *Elymus elymoides*, McBride et al., Natl. Tech. Inf. Serv. IDO–12084, 1978). Mean elevation of the burn site is 1515 m. A more detailed description of the physical and biotic environments of the study area is given in Gates (M.S. thesis, Montana State Univ., Bozeman, Montana, 1983).

Four hundred ha of the study area were control-burned in Aug. and Oct. 1981. Prior to burning, arenas occurred on (Arena A) and adjacent to (Arena B) the burn site. Ten male grouse were captured (Giesen et al., Wildl. Soc. Bull. 10:224–231, 1982) on Arena B in 1981; 10 males and five females were marked there in 1982. Five males and one female were marked on Arena A in 1982. Seventy grouse were captured and marked on three other arenas within 6.5 km of the burn site. In addition, 113 grouse were marked in irrigated cropland 6.4 km north of the burn site. Captured grouse were marked with numbered patagial tags (males), poncho tags (females; Pyrah, J. Wildl. Manage. 34:466–467, 1974), or radio-collars (both sexes; Amstrup, J. Wildl. Manage. 44:214–217, 1980).

Five arenas within 6.5 km of the burn site were censused in the springs of 1981–1983. The maximum number of males attending Arena B declined from 45 in 1981, to 25 in 1982, and 18 in 1983. Arena A, which was used by grouse in 1981 but not censused, declined from 12 males in 1982 to three in 1983. A similar decline of males from 39 to 20 to 16 occurred between 1981 and 1983 on an arena 6.5 km east of the burn site. No grouse were observed in 1982 and 1983 on an arena 3.5 km southeast of the burn site that had 18 males in 1981. The apparent cause of the downward population trend between 1981 and 1983 was poor production resulting from abnormally cold, wet weather during the springs of 1980 and 1981 (Gates 1983).

A new arena (Arena C) was discovered on the burn site on 10 Apr. 1982, 1.5 and 2.0 km south of Arenas A and B. Arena C was observed on six mornings between 10 and 29 Apr.

1982. Grouse were present on four mornings through 23 Apr. Three males and 7–11 females were observed on three mornings from 10 through 16 Apr. A fourth male appeared on the periphery of Arena C on 23 Apr.; however, no females were present. No grouse were observed on two subsequent visits to Arena C on 24 and 29 Apr.

One of the males (M510) initially observed on the new arena was wing-tagged as a juvenile in irrigated cropland 8 km to the north in July 1980. He was recaptured on Arena B, adjacent to the burn site, on 28 Mar. 1981 and was seen again on the same arena on 27 Mar. 1982. In 1982, this bird did not occupy even a peripheral territory on the arena, which was attended by 20–25 males. He was unable to defend a breeding territory and was displaced continually by other males as described by Wiley (Anim. Behav. Monogr. 6:85–169, 1973:135).

Fourteen days after being seen on Arena B in 1982, M510 was observed occupying a central territory on Arena C, which he defended against two other males. Seven females present on 10 Apr. 1982 remained mostly within the area that M510 defended. On 16 Apr., M510 was observed copulating with one of 8 females in attendance. None of the other three displaying males was observed to copulate during three mornings of observation when hens were present.

Both males captured on the new arena on 12 Apr. 1982 were adults (>1 year), based on the condition and shape of their 9th and 10th primaries (Dalke et al. 1963). Both males were observed displaying with M510 on 16 and 23 Apr. 1982. They may have been the same individuals observed with M510 on 10 Apr. Three females captured on the new arena on 17 and 18 Apr. were yearlings, based on the appearance of their outer two primaries.

In Apr. 1983, the new arena could be censused only by flushing the birds from small burned openings in the sagebrush 30–75 m from the area that was used in 1982. The reason for this shift from the more open area used in 1982 to a smaller burned area in 1983 was unknown. Vegetation regrowth was minimal one year after burning. A maximum of five males and three females was observed on the new arena in April 1983. One or two wing-tagged males were observed each morning that the arena was visited; however, their identities were not determined.

Connelly et al. (1981) documented Sage Grouse displaying on recently disturbed sites elsewhere on the INEL during 1978 and 1979, a period of increase in the grouse population. I observed grouse displaying and mating on a burned area during the first two breeding seasons following a burn and during a population decline. At least three of four males attending the arena in its initial year were adults and three captured females were yearlings. Up to 11 females were observed in attendance daily in 1982, so some adults could have been present.

Eng et al. (pp. 464–468 *in* The Mitigation Symposium, Colorado State Univ., Fort Collins, Colorado, 1979) reported that most of the first females to attend a new arena were yearlings. Adult females show a certain degree of fidelity to arenas that they attended in previous years (Dalke et al., Trans. N. Am. Wildl. Nat. Resour. Conf. 24:396–407, 1960), although movements between arenas within and among years is common (Wallestad, Life History and Habitat Requirements of Sage Grouse in Central Montana, Montana Dept. Fish and Game, Helena, Montana, 1975; Petersen, M.S. thesis Colorado State Univ., Fort Collins, Colorado, 1980).

Adult males show greater fidelity to arenas than do females (Dalke et al. 1960; Emmons, J. Wildl. Manage. 48:1023–1028, 1984). Although young males are physiologically capable of breeding (Eng. J. Wildl. Manage. 27:841–849, 1963), their subordinate position on previously established arenas affords them a low probability of mating (Wiley 1973). I observed a 2-year-old male that colonized and copulated on a new arena. By colonizing new openings and attracting females, some young males may enhance their opportunities for breeding in the short- and long-term. The first males to colonize new arenas may be young adults not firmly established as members of other breeding populations. Yearling males, however,

appear to be attracted to arenas by the presence of grouse of both sexes (see Wiley 1973). Eng et al. (1979) reported that yearling males were the first to be attracted to an artificial arena on which decoys were placed and recorded sounds of displaying grouse were played.

Females were captured on the new arena at a time of year when yearling hens normally predominate on INEL leks; however, breeding phenology was delayed 2–3 weeks in 1982 by adverse weather. Adult females were captured on nearby arenas as late as 18 Apr. and yearlings were first captured on 10 Apr. The delayed breeding season may have caused more overlap in the appearance of yearling and adult hens on arenas and may, in part, explain the success of the new arena in attracting females in 1982. Hannon et al. (Auk 99:687–694, 1982) implicated aggressive behavior of adults as the cause for delayed breeding and greater distances traveled to nest by yearling Blue Grouse (*Dendragapus obscurus*). With reduced competition from adults on new leks, yearling female Sage Grouse could establish more easily a tradition of breeding on new arenas.

The appearance of displaying grouse on recently disturbed sites suggests that natural openings suitable for arenas are limited on some areas of the INEL. Sagebrush-dominated vegetation types cover most of the western INEL but openings occur in playas, shallow basins, and disturbed areas. Of nine arenas within 12 km of the burn site, four occur in playas or basins and five are on burned areas. Eng et al. (1979) stressed the importance of juxtaposition of arenas with winter, nesting, and early brood-rearing habitat. In areas such as the western INEL where sagebrush cover is continuous over large areas and openings are widely spaced, suitable nesting and early brood-rearing habitat may be underused due to isolation from arenas; however, this needs to be demonstrated.

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Nest usurpation and female competition for breeding opportunities by Tree Swallows.—Tree Swallows (*Tachycineta bicolor*) are hole nesters that are often limited by nest site availability (Holroyd, Can. Field-Nat. 89:60–64, 1975). Populations generally increase following the erection of nest boxes (Low, Bird-Banding 3:76–87, 1933; Chapman, Bird-Banding 6:45–57, 1935; Holroyd 1975), and competition for nest-sites occurs early in the breeding season (Kuerzi, Proc. Linn. Soc. N.Y. 52–53:1–52, 1941). Territorial defence of the area surrounding the nest-site may further limit the availability of breeding opportunities if more than one nest-site is defended by a single pair of birds. Harris (Can. J. Zool. 57: 2072–2078, 1979) argued that the defense of unnecessary resources (extra boxes) was an example of superterritoriality (Verner, Am. Nat. 111:769–775, 1977). Robertson and Gibbs (Condor 84:313–316, 1982), however, found that territorial defense was not focused on

extra boxes and therefore has probably evolved as the most effective way to defend the single nest-site required for breeding, rather than as a superterritorial strategy.

Clearly, nest-site limitation leads to aggressive interactions among Tree Swallows, and territorial defense can prevent conspecifics from breeding even when unoccupied boxes are present (Harris 1979). It is generally assumed that competition for nest-sites involves defense of the nest by both members of the pair (Harris 1979, Robertson and Gibbs 1982). Here, we report several instances of nest-site usurpation by females. These indicate a lack of cooperative defense by the pair and suggest that females may be competing for breeding opportunities involving a male with a nest-site, rather than a nest-site per se.

During the summer of 1982, we studied the breeding ecology of Tree Swallows at Queen's University Biological Station near Chaffey's Lock, Frontenac Co., Ontario. The study site consisted of four hayfields and a nearby pond. There were 139 nest boxes distributed over this area. In three of the fields and in the pond some of the boxes were arranged in spirals, so that there were boxes 1, 2, 4, 8, and 16 m away from a central box (see Robertson and Gibbs 1982). Additional boxes were interspersed between these spirals with a minimum interbox distance of 16 m. A total of 47 clutches hatched, and an additional eight clutches were incomplete, abandoned, or infertile. The nest box occupancy rate for the entire season was 40% (55/139). Both early in the season, while nest-sites were being established, and later during the incubation and nestling periods, interactions between members of resident pairs, and between resident pairs and intruders, were observed. Eighty-four percent of the breeding females and 46% of the males were color-marked for individual identification.

The first nest-site usurpations occurred on May 12, while most females were building nests. Two color-marked females, female-A and female-B, were attacked and evicted from their boxes by other individuals (one of which was positively identified as a female). Both of the evicted females were in their second or later season after hatching (after-second-year, or ASY), and both had been paired for at least 2 weeks. Following the evictions, the resident females were found on the ground after fighting, too weak to fly and with feathers missing from their crowns and napes. Female-A flew weakly into some nearby brush. Female-B was removed by the observer and placed under shelter, where she later recovered and then flew off. New females were seen with the original males. Female-A was replaced by an ASY female, and female-B was replaced by two females, an ASY and a SY (second–year female, in the first season after hatching). This was the only bigamous mating on the study site. Both ASY females successfully raised broods. The SY female raised a brood of five nestlings, apparently without help, to d 15 and then abandoned the nest after being captured for banding. Abandonment after handling was rare, especially when handling occurred late in the nesting cycle (Burtt and Tuttle, J. Field Ornithol. 54:319–323, 1983), suggesting that this female may have been unusually stressed by having to rear her brood alone. The growth rate of her nestlings was much lower than average (day 14 mean weight = 14.8 ± 2.17 g [SD] [range 12.5–17.5 g] compared with day 14 mean weight = 22.9 ± 1.43 g [range 19.0–26.0 g] for eight other nests with five or more nestlings), indicating that the unassisted female might have been unable to provide sufficient food. Evicted female-A reappeared on May 16 paired with a previously mated male at a nest box 100 m from her original nest. Whether usurpation was involved in this case is unknown. She successfully raised a brood with this male.

A second series of usurpations occurred during incubation. Female-B reappeared on June 5 at a nest box that had previously been occupied by an incubating female, 25 m from her original box. No aggressive interactions between female-B and the displaced pair were witnessed, although the pair remained in the vicinity. Six eggs laid by the previous female had been covered with new nesting material. Female-B subsequently laid a clutch of her own that hatched but was later abandoned. No male was ever seen with female-B during

this nesting attempt. The pair evicted by female-B moved 30 m to a spiral of boxes in which another pair was incubating a seven-egg clutch. After much aggressive interaction, both pairs renested successfully within the same spiral, 16 m apart, with the incoming pair occupying the box containing the clutch of the original pair. They laid their new clutch directly in the nest cup containing the original seven eggs.

The final series of usurpations occurred during the nestling stage, when a number of new SY females arrived in the area. Three paired ASY females were evicted, apparently without aggressive interactions. The males of these three pairs were seen in the company of new SY females and subsequently their ASY mates abandoned their broods. In one of the three cases, however, it is possible that the disappearance of the original female was due to some other cause, since she was not seen again, and may have died. Two of the new pairs raised broods in the same boxes as broods from the previous matings; the dead or dying nestlings had been removed by the observer.

These interactions raise questions concerning the mating strategies of both male and female Tree Swallows. During the study, there was an excess of nest boxes. Boxes less than 18 m from occupied boxes cannot be considered "available" as nest sites, because Tree Swallows defend territories of approximately 18-m radius (Robertson and Gibbs 1982). Nevertheless, 5 of the 22 boxes interspersed between sprirals, which were more than 18 m from other boxes, remained unused. Furthermore, Tree Swallows do sometimes nest less than 18 m apart: Harris (1979) had up to four pairs nesting in a spiral similar to ours, and we frequently had two pairs nesting at either end of a spiral, approximately 18 m apart. This indicates that it could not be a shortage of available nest-sites per se that causes the usurpations. We suggest rather that it is a shortage of males with nest boxes that brings about competition between females.

During the first and third series of usurpations, females displaced one another, while the males remained at the original nest-sites and remated with the successful females. This suggests that males may claim a nest box and territory and allow females to compete to become their mates. Whether there is actually a shortage of males is unclear. Three females did partially raise broods without a partner while unused boxes were available, suggesting that some females were unable to mate monogamously. Further experiments, however, have shown that if new boxes are erected later in the breeding season, they are occupied by mated pairs of Tree Swallows rather than by lone females (Stutchbury and Robertson, Auk, in press). Further study is needed to determine the actual secondary and operational sex ratios in this species.

The pattern of plumage dimorphism in SY birds might suggest an operational sex ratio skewed toward females. Tree Swallows are the only North American passerines in which females have a distinct subadult plumage (Rohwer et al., Am. Nat. 115:400–437, 1980). SY females have a dull brown, juvenile-like plumage, while ASY females and all males have an irridescent dark blue plumage (Low 1933; Kuerzi 1941; Hussell, J. Field Ornithol. 54: 312–318, 1983). Subadult plumage in males occurs in several species of North American passerines, and the analysis by Rohwer et al. (1980) indicates that a shortage of females is one of the most important contributing factors. Delayed plumage maturation in female Tree Swallows may therefore imply a shortage of males, or at least a shortage of breeding opportunities for females. Studies are underway to determine whether the brown plumage of SY females gives them an advantage in gaining access to breeding opportunities.

It is noteworthy that site dominance does not prevent evictions in Tree Swallows. Possibly there is an asymmetry in the ability to forage, and therefore in physical condition, between the incubating/brooding female and the intruding female. In the absence of dangerous weapons, fighting is essentially without risk (Rohwer, Am. Zool. 22:539–546, 1982), and is therefore primarily a battle of endurance (but see Brown, Bird-Banding 48:273, 1977). If

breeding females lose weight (De Steven, Evol. 34:278–291, 1980), their reserves of energy may be depleted by the time later females arrive.

Why males do not defend against intruding females, but rather are willing to mate with them at the expense of losing their initial mate part of the way through incubation or brooding, remains to be explained. This is especially puzzling with respect to intruding SY females, as these have been shown to have lower reproductive success than ASY females (De Steven, Ibis 120:516–523, 1978). In our study, the three males that mated with SY females after the eggs laid by their original ASY mates had hatched all fledged fewer young with the new SY females than they would have had they remained with their ASY mates. This pattern of mate change has also been found in other studies on the Tree Swallow (Shelley, Bird-Banding 6:33–35, 1935).

In our study area, it appears that both parents are needed to fledge a full brood of nestlings (Leffelaar, M.Sc. thesis, Queen's University, Kingston, Ontario, Canada, 1983); perhaps this explains why the three females referred to above did not persist in trying to raise their nestlings alone, while their mates were consorting with new SY females. Two parents may be needed for feeding nestlings because there may be a low food supply in our study area. At Long Point, Ontario, where the food supply is greater, there is evidence of a higher incidence of polygyny. That there is a greater food supply at Long Point is suggested by the lower brood success (75%) found in our study area as compared with that found at Long Point (95% and 88%) by De Steven (1980) and Quinney (1983), respectively. Quinney (Auk 100:750–754, 1983) found several cases where two females were mated with a single male and nested together in a single box. This also supports the contention that the operational sex ratio may be skewed towards females.

Polygyny may thus be a strategy pursued by males under conditions of high food abundance, explaining why males do not assist in defense against intruding females. In areas with lower food availability monogamy may be required. This in turn may have led to female competition for the limited number of potential mates possessing nest sites. Whether the apparent decrease in reproductive success of those males which abandoned their mates during the nestling period is a result of an inferior reproductive strategy, or is due to some other as yet unknown factor, has yet to be determined.

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Wintering Bald Eagles along the Rio Yaqui, Sonora, Mexico.—Wintering Bald Eagles (*Haliaeetus leucocephalus*) in Mexico have been recorded only from the coasts of Baja California and from the Sonoran coast of the Gulf of California (Brown and Amadon, Eagles, Hawks and Falcons of the World, Vol. 1, McGraw-Hill, New York, New York, 1968). Inland sightings of Bald Eagles in western Mexico are rare, and wintering areas for the species west of the continental divide have not been reported, probably because ornithologists visit the area infrequently (G. Monson, S. M. Russell, pers. comm.). This note provides information on the status of Bald Eagles wintering along the Rio Yaqui drainage of Sonora, Mexico.

Controlled water releases since construction of a dam in the mid-1960s guarantee relatively

FIG. 1. Study area for Bald Eagle censuses along the Rio Yaqui, Sonora, Mexico.

uniform, high-volume flow on the Rio Yaqui below the El Novillo reservoir. Above the reservoir, and particularly above the Aros/Bavispe confluence, flow is highly seasonal with a peak from August to October and a low from December to June. Although a smaller dam on the Rio Bavispe at Angostura may stabilize the flow above El Novillo to some extent, portions of the upper river are sometimes dry during winter and spring.

The authors made five censuses by boat on various stretches of the Rio Yaqui and its tributaries from December 1981 to December 1983 (Fig. 1). Three censuses were in winter, and two were in summer. Two winter censuses (31 Dec. 1981 to 7 Jan. 1982; 31 Dec. 1982 to 8 Jan. 1983) were conducted along the 160-km stretch from the El Novillo reservoir to the Alvaro Obregon reservoir near Obregon. The third winter census, from 12 to 19 Dec. 1983, was made from Huasabas on the Rio Bavispe to its confluence with the Rio Aros, and from there to the head of the El Novillo reservoir, a distance of 145 km. Summer censuses were made along a 70-km route from the El Novillo dam to Tonichi on 10–15 Sept. 1982 and 31 Aug. to 5 Sept. 1983. The location, date of observation, and number of all eagles sighted were recorded. Approximately 20 km of river were censused each day by two to six experienced observers. The relatively long length of the census periods, up to eight days, meant that some eagles may have been counted on more than one day.

Seven Bald Eagles were seen during the 1981–82 census: three adults near Soyopa on 2 Jan. 1982 below the El Novillo Reservoir; two immature eagles (individuals with white mottling and lacking a white head) and an adult below Soyopa on 3 Jan.; and one adult above Tonichi on 3 Jan. At least four adults were seen during the 1982–83 census: one adult was seen 16 km below the dam on 1 January 1983; another adult observed at the same locality a few hours later could have been the same individual; two adults were seen on 2 Jan. near Soyopa; and one immature was seen on 3 Jan. below Soyopa. The early winter trip of 1983 produced a single sighting of an adult on 14 Dec. at the mouth of the Arroyo Bacadehuachi, approximately 120 river-km above the El Novillo reservoir. No Bald Eagles were seen on either summer trip.

In addition to our observations, we spoke with local residents along the river near El Novillo. They were familiar with *Aguilas de Cabeza Blanca* (Bald Eagles) and had observed them fishing in the reservoir in prior years.

The distribution of Bald Eagles along the Rio Yaqui prior to construction of the dam is unknown. Based on our observations and local interviews it is evident that Bald Eagles now are regular winter residents in small numbers along the Rio Yaqui drainage, especially below the El Novillo dam. The Rio Yaqui locality represents the only area of inland Sonora where Bald Eagles are known to occur regularly in winter, and it is the southern-most known wintering location west of the continental divide in North America.

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Food habits of Richardson's Merlins in southeastern Montana.—Early information on food habits of Merlins (*Falco columbarius*) in North America was derived primarily from examination of stomach and crop contents (Fisher, U.S.D.A. Bull. No. 3., 1893; Bent, U.S. Natl. Mus. Bull. 170, 1938), observation of hunting and feeding activities (Craighead and

Craighead, Wilson Bull. 52:241–248, 1940; Lawrence, Wilson Bull. 61:12–25, 1949), and examination of regurgitated pellets (Breckenridge and Errington, Auk 55:668–670, 1938; Johnson and Coble, Jack-Pine Warbler 45:97–98, 1967). Food habits of breeding Merlins have also been examined and quantified by analyses of prey remains gathered at or near active nests, both in Canada (Fox, Blue Jay 12:140–147, 1964; Oliphant and McTaggart, Can. Field-Nat. 91:190–192, 1977; Hodson, Can. Field-Nat. 92:76–77, 1978) and in Europe (Sperber and Sperber, Zoologiska Bidrag Fran Uppsala 35:263–268, 1963; Newton et al., Br. Birds 71:376–398, 1978; Watson, Bird Study 26:253–258, 1979). To date, little is known about the food habits of Merlins breeding in the western United States. This paper reports food habits of Richardson's Merlins (*F. c. richardsonii*) breeding in southeastern Montana during 1980 and 1981.

Study area and methods.—Merlins were studied in southeastern Montana in an area dominated by hills and sandstone buttes ranging to approximately 300 m above adjacent prairies and farmlands. Grassland comprised approximately 67% of the 39,448 ha study area, while 27% was covered by forest. The remaining 6% was composed of rough, broken badlands habitat. Forested habitat was dominated by ponderosa pine (*Pinus ponderosa*) associated with aspen (*Populus tremuloides*), box elder (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*). Grasslands were composed largely of blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron smithii*), and needle-and-thread grass (*Stipa comata*). Dominant shrubs were big sagebrush (*Artemisia tridentata*), silver sagebrush (*A. cana*), and snowberry (*Symphoricarpos albus*).

From May through July 1980 and 1981, prey remains (contour feathers, wings, legs, beaks, etc.) and regurgitated pellets were collected at and near 20 active Richardson's Merlin nests. Each nest was visited three to five times, and all prey remains at the nest-site and at nearby perches were collected. Prey remains were identified to species when possible. Primary feathers were counted individually. Based upon comparisons with museum specimens, if fewer than the expected number of primaries of a left or a right wing were present, it was assumed that one individual bird had been consumed. When more than the expected number of primaries from a left or a right wing were located, these were counted, divided by the number of primaries for that species, and rounded to the next highest number to provide the number of individual prey involved (Page and Whitacre, Condor 77:73–83, 1975).

Pellets were examined under a variable power dissecting microscope. Bird and reptile remains were compared with museum specimens in the University of Montana Zoology Museum. Skulls of mammals were identified using a skull key (Hoffman and Pattie, Univ. Montana Printing, 1968). Hair samples were identified by dorsal guard hair characteristics (Moore et al., Wyoming Game and Fish Dept. Bull. 14, 1974). Insect remains were compared with specimens collected in the field. Weights of bird and mammal prey were obtained from information recorded for museum specimens in the University of Montana Zoology Museum. Weights for insects were obtained from specimens collected in the field.

Food habits.—A total of 1951 individual prey items (flight feathers, wings, legs, beaks, etc.) and 110 pellets were collected from nests and perches during 88 visits. These items represented at least 173 prey in 1980 and 254 in 1981.

Birds comprised 393 (92%) of the prey items and 93% of the total biomass of prey (Table 1). Seventeen (61%) of 28 species of birds identified as prey were species typically associated with grasslands or predominantly open prairie habitats. These species represented 83% of the total number of individual prey and 83% of the total biomass. Horned Larks (*Eremophila alpestris*) and Lark Buntings (*Calamospiza melanocorys*) each comprised 21% of the total biomass, and Vesper Sparrows (*Pooecetes gramineus*) were approximately 10%. Western Meadowlarks (*Sturnella neglecta*) comprised only about 4% of the total prey, but accounted for 12% of the biomass. Seven prey species were associated with forested habitat. These species represented 7% of the total prey and 10% of the total biomass.

TABLE 1

MAJOR PREY SPECIES OF RICHARDSON'S MERLINS IN SOUTHEASTERN MONTANA, 1980–1981

	No. of individuals	% total	Biomass (g)	% biomass
Birds				
Horned Lark (*Eremophila alpestris*)	116	27.2	3062	21.2
Lark Bunting (*Calamospiza melanacorys*)	75	17.6	3023	21.0
Vesper Sparrow (*Pooecetes gramineus*)	54	12.6	1366	9.5
Mountain Bluebird (*Sialia currocoides*)	28	6.6	644	4.5
Western Meadowlark (*Sturnella neglecta*)	18	4.2	1728	12.0
Chestnut-collared Longspur (*Calcarius ornatus*)	16	3.7	272	1.9
Red Crossbill (*Loxia curvirostra*)	13	3.0	419	2.9
American Goldfinch (*Carduelis tristis*)	9	2.1	132	0.9
Chipping Sparrow (*Spizella passerina*)	7	1.6	84	0.6
Killdeer (*Charadrius vociferus*)	7	1.6	728	5.0
Unidentified birds	6	1.4	229	1.6
Bobolink (*Dolichonyx oryzivorous*)	5	1.2	165	1.1
Brown-headed Cowbird (*Molothrus ater*)	5	1.2	220	1.5
Brewer's Sparrow (*Spizella breweri*)	5	1.2	60	0.4
Brewer's Blackbird (*Euphagus cyanocephalus*)	5	1.2	340	2.4
Lark Sparrow (*Chondestes grammacus*)	4	0.9	92	0.6
Townsend's Solitaire (*Myadestes townsendi*)	4	0.9	130	0.9
Other birds[a]	16	3.7	725	5.0
Subtotals	393	91.9	13,419	93.1
Other				
Grasshopper (Acrididae)	17	4.0	17	0.1
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	8	1.9	920	6.4

TABLE 1
CONTINUED

	No. of individuals	% total	Biomass (g)	% biomass
Moth (Noctuidae)	5	1.2	7	<0.1
Other mammals and reptiles[b]	4	0.9	62	0.4
Subtotals	34	8.0	1006	7.0
Totals	427	100.0	14,425	100.0

[a] Including one or two individuals of the following: House Sparrow (*Passer domesticus*), Common Poorwill (*Phalaenoptilus nuttallii*), Red-winged Blackbird (*Agelaius phoeniceus*), American Robin (*Turdus migratorius*), Cliff Swallow (*Petrochelidon phyrrhonota*), Eastern Kingbird (*Tyrannus tyrannus*), Savannah Sparrow (*Passerculus sandwichensis*), Dark-eyed Junco (*Junco hyemalis*), Northern Oriole (*Icterus galbula*), Mourning Dove (*Zenaida macroura*), and Yellow-rumped Warbler (*Dendroica coronata*).

[b] Including one or two individuals of the following: myotis (*Myotis* spp.), least chipmunk (*Eutamias minimus*), and northern short-horned lizard (*Phrynosoma douglassi brevirostre*).

The only insects recorded as prey were grasshoppers (Acrididae) and moths (Noctuidae), which comprised 5% of the prey (Table 1). Mammals, mostly thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), accounted for approximately 3% of the prey. the only reptile recorded was one northern short-horned lizard (*Phrynosoma douglassi brevirostre*). A comparison of individual prey species consumed by Merlins in 1980 (33) and in 1981 (23) indicated that the relative composition of prey species was similar ($r_s = 0.62$, $P \leq 0.05$) between years.

This study illustrates the importance of grassland/prairie avifauna as a major prey component of breeding Richardson's Merlins in southeastern Montana. Similar results have been recorded in studies of food habits of Merlins breeding in the Canadian prairies. Fox (Blue Jay 12:140–147, 1964) observed that about 54% of the prey items noted in his study area in Saskatchewan were Horned Larks. Hodson (Can. Field-Nat. 92:76–77, 1978) found that 50% of prey items collected in Alberta consisted of the remains of Horned Larks.

A radio-telemetry study of breeding male Richardson's Merlins on the Montana study area indicated that the birds hunted most often in open sagebrush/grassland habitats (Becker, M.S. thesis, Univ. Montana, Missoula, Montana, 1984). Horned Larks, Lark Buntings, and Vesper Sparrows were the most conspicuous species and possibly the most abundant in these habitats. Hodson (1978) hypothesized that breeding Richardson's Merlins in Alberta preyed heavily on Horned Larks and Chestnut-collared Longspurs (*Calcarius ornatus*) because the feeding methods of these passerines made them more noticeable than other grassland birds. Oliphant and McTaggart (1977) suggested that Merlins breeding in urban Saskatoon, Saskatchewan, were taking a large number of House Sparrows (*Passer domesticus*) (64% of 176 identified prey items) because this species was abundant at the time.

Although Horned Larks represented a large proportion of Merlin prey documented in this study, 32 other species were also taken by Merlins. Conspicuous, abundant grassland birds were caught most often by Richardson's Merlins, and avifauna associated with forest communities was less prevalent in the diet. The variety of foods in the diet of Richardson's Merlins in southeastern Montana is probably a reflection of the diversity of habitats on the study area.

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Raptors killing raptors.—There are few detailed accounts of diurnal raptors killing other diurnal raptors (Peyton, Condor 47:167, 1945; Broun, Hawks Aloft: The Story of Hawk Mountain, Dodd, Mead Co., New York, New York, 1949:193–194; Rudebeck, Oikos 2:65–88, 1950; Rudebeck, Oikos 3:200–231, 1951). Here we provide additional field observations of this type of killing and suggest why it occurs.

Our observations were made during a study of the individual flight patterns of migrating raptors at Lehigh Gap, a break in the Kittatiny Ridge at Palmerton, Pennsylvania.

At 13:10, 15 Oct. 1982, a Peregrine Falcon (*Falco peregrinus*) was seen flying over the northeastern edge of the gap. The size of the falcon suggested it was a female. For approximately 2 min it coursed over the edge. It then turned west and set its wings in a gliding position. Suddenly, the falcon captured a Sharp-shinned Hawk (*Accipiter striatus*) believed to be a male because of its small size. The hawk was also in a glide prior to capture. The falcon approached its quarry from below (15–30 cm) and then flew up, flared its wings, and grasped the back of the accipiter. The hawk did not struggle after being grasped, and fell limp. The Peregrine Falcon then turned and flew back to the northeastern edge of the gap using labored flapping flight.

W. S. Clark and P. Dunne (pers. comm.) witnessed a Peregrine Falcon capture a Sharp-shinned Hawk in the fall of 1976 at their Cape May Point, New Jersey, banding station. The victim was gliding into a trap area when an immature male falcon struck it from above. As the Peregrine Falcon carried off its prey, a Northern Harrier (*Circus cyaneus*) began chasing the falcon. The peregrine responded by flying swiftly and turning sharply from side to side. Both birds passed from view over grass and dunes. Within a few seconds the falcon bolted almost straight up into the air without its prey.The harrier did not reappear.

D. F. Brinker and T. C. Erdman (pers. comm.) watched a Red-tailed Hawk (*Buteo jamaicensis*) capture a Sharp-shinned Hawk at their banding station on the west shore of Green Bay, Wisconsin. They also stated that during migration the larger raptors such as Red-tailed Hawks are lured to traps by previously captured smaller raptors such as Sharp-shinned Hawks. The larger birds dropped from their passage, entered the traps, and killed the smaller birds.

While banding raptors between 9 and 22 Oct. 1974, J. Ruos (pers. comm.) observed raptors of several species hunting other species on Loggerhead Key, Dry Tortugas, Florida. The weather was unfavorable for migration, with high winds and seas, and few typical prey were available to the predators. On several occasions during 11 Oct. Sharp-shinned Hawks attacked other Sharp-shinned Hawks caught in mist nets. Between 13 and 21 Oct. observations of Peregrine Falcons chasing a Sharp-shinned Hawk, American Kestrels (*F. sparverius*), and a Merlin (*F. columbarius*) suggest that the pursuing raptor was attempting to prey on the smaller ones.

Smaller raptors have also killed larger ones. From different accounts, Forbush (Birds of Massachusetts and Other New England States, Part II, Norwood Press, Norwood, Massachusetts, 1927:170) describes Peregrine Falcons killing Red-shouldered Hawks (*B. lineatus*)

and a Snowy Owl (*Nyctea scandiaca*). The suggested motives were nest defense against the hawks and defense of young against the owl. An additional account occurred in March 1981 during the spring migration just south of Albany, New York. T. K. Judge (pers. comm.) witnessed a Merlin strike and kill a Red-tailed Hawk. The Merlin was watched for approximately 20 min prior to the assault. The falcon initiated its attack from a perch in a tree, and struck the larger bird in mid-air. The Red-tailed Hawk lost some feathers, appeared limp and lifeless, and immediately dropped to the ground. No motive for this killing was evident.

Suggested motives for interspecific killing by raptors are competition for territory, food, or breeding sites (Mikkola, Br. Birds 69:144–154, 1976). Rudebeck (1951), referring to large raptors attacking smaller ones, suggested that the conspicuousness of some raptors might make them more vulnerable to larger ones, especially on migration when large numbers of raptors regularly interact while traveling in close proximity. In addition, large raptors kill smaller ones for what has been described as annoyance (p. 141, Brown and Amadon, Eagles, Hawks and Falcons of the World, McGraw-Hill Book Co., New York, New York, Vol. 1, 1968).

In sum, field observations suggest that raptors kill other raptors for food, in self-defense, and in defense of territories, nests, and young.

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Ants and foraging behavior of the Collared Forest-Falcon.—Few details concerning the habits of the Collared Forest-Falcon (*Micrastur semitorquatus*) are known. A nest was described recently by Mader (Condor 81:320, 1979). An egg, laid by a captive falcon, was described by Wetmore (Condor 76:103, 1974). Birds, lizards, and snakes have been reported as prey (Sutton and Pettingill, Auk 59:1–44, 1942; Wetmore, Smithson. Misc. Coll. 150: 266–268, 1965; Smithe, The Birds of Tikal, Natural History Press, Garden City, New York, 1966). Smith (Ibis 111:241–243, 1969) suggested that the Collared Forest-Falcon calls to provoke mobbing by small birds in order to capture them, and mentioned that *Micrastur* falcons are attracted to the sounds made by excited birds such as those following swarms of army ants. The Barred Forest-Falcon (*M. ruficollis*) is a "persistent ant follower that terrifies small birds, but mostly captures large insects" (Willis and Oniki, Ann. Rev. Ecol. Syst. 9:243–263, 1978). Slud (Bull. Am. Mus. Nat. Hist. 128:70–72, 1964) stated that Barred Forest-Falcons are attracted to swarms of army ants to prey on the attendant small birds. Skutch (New Studies of Tropical American Birds, Nuttall Ornithol. Club, Cambridge, Massachusetts, 1981) observed an immature Collared Forest-Falcon following army ants, eating large insects and spiders, and ignoring the small birds present. Here, I report three incidents of a mature Collared Forest-Falcon at swarms of ants.

My observations of Collared Forest-Falcons and ants occurred at Monteverde, Costa Rica,

in the surrounding premontane moist semideciduous forest at an elevation of 1300–1400 m in the dry season in March 1983. All three observations were made within an area of approximately 0.5-ha. I used a pair of 9 × 36 binoculars. Two species of ants were involved, but no specimens were collected for identification. The army ants that attracted the falcon were small and black and moved in columns that radiated like fingers from a hand. The second species of ant involved in the observations was not an army ant. The latter moved back and forth in a column, along trails, not steadily ahead as did the army ants.

I first observed a falcon in mature plumage foraging at an army ant swarm on 11 March. It perched 0.2–0.5 m above the ants and intently watched the column. Three times the bird dropped to the forest floor, scratched in the litter first with one foot, then the other, pecked at insects fleeing the ants, and returned to its perch just above the forest floor. Although I was able repeatedly to approach within 3–9 m of the falcon, I was unable to see if prey was taken. Finally, the falcon dropped into the army ant swarm, scratched vigorously, fluffed up its feathers and squatted down on the ants, much like a brooding hen, for 45–60 sec. The falcon then hopped to a low perch, picked two ants off its toes and flew away.

On 18 March, I watched a Collared Forest-Falcon foraging near a column of non-army ants for a period of 35 min. I saw it pick up arthropods near the ants and heard crunching noises as it ate. Consistent with the previous observation on 11 March, the falcon perched on low branches (0.3–2 m above ground) and made sallies (N = 6) to the ground to pick up insects and other small items, returning to a low perch each time.

My final observation occurred on 21 March. Some lizards and large numbers of insects and spiders were fleeing a swarm of army ants. A Collared Forest-Falcon perched quietly about 0.3 m above the swarm. I watched the falcon for 38 min. The foraging technique of the falcon was similar to that in the two previous episodes. It sallied to the ground (N = 11) from low perches (0.1–1 m); but the bird spent much more time on the ground than in the previous two episodes, actually running after prey, sometimes with half-opened wings. I saw it pounce (N = 4) on arthropods and lizards with both feet and then pick the prey from under its toes with its bill and eat. Three times the falcon did a brief staccato "tap dance" alternately with each foot, and occasionally scratched itself with one of its feet. My impression was that the bird was attempting to dislodge ants crawling up its feet and legs. It ignored my presence and foraged to within 2.5 m of me on several occasions.

No small birds appeared to be following the army ant swarms observed, although several species of migrant and resident birds that frequently follow army ants (Willis 1966; Hilty, Wilson Bull. 86:479–481, 1974; Willis and Oniki 1978) were present in the area. Two Long-tailed Manakins (*Chiroxiphia linearis*) sang 3 m above the falcon during the second observation with no apparent interaction between the species. The observation of a wild Collared Forest-Falcon, scratching in the litter, and running on the ground after prey, often with half-opened wings, corroborates the report of Peeters (J. Ornithol. 104:357–364, 1963) on the foraging behavior of two captive Collared Forest-Falcons in California, and is similar to a description of ant-following by *M. ruficollis* (Willis, Wechsler and Stiles, Rev. Brasil. Biol. 43:23–28, 1983). The technique of making sallies from a low perch is the most common foraging pattern used by ant-following birds (Willis, Wilson Bull. 94:447–462, 1982).

The 11 March observation may be the first report of passive anting by a wild raptor. A description of anting by a captive Great Horned Owl (*Bubo virginianus*) was cited by Whitaker (Wilson Bull. 69:195–262, 1957).

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Caspian Terns respond to rattlesnake predation in a colony.—Colonial living potentially enhances predator detection and defense by increased response to intruders. Responses may vary according to the vulnerability of the prey (Leger and Nelson, Wilson Bull. 94:322–328, 1982) and the species of predator (Seyfarth, Cheney, and Marler, Science 210:801–803, 1980). Black Skimmers (*Rynchops niger*) and Caspian Terns (*Sterna caspia*) nesting on dredged material islands in Lavaca Bay, Calhoun Co., Texas (March–July, 1982 and 1983) were subject to predation by western diamondback rattlesnakes (*Crotalus atrox*). Here, I report evidence for predation on Black Skimmers by rattlesnakes, and observations of the responses of adult Caspian Terns to a rattlesnake.

On 14 June 1983, I captured a western diamondback rattlesnake (about 1.25 m long) adjacent to an about 15-d old dead Black Skimmer chick. A necropsy revealed a hematoma on the back of the chick associated with two holes, 1 mm in diameter and 1–1.5 cm apart, in the musculature at the base of the neck. These were virtually identical to fang marks produced by an induced bite on the breast of the chick by the same snake. Also within 5 m of the snake was a dead adult male Black Skimmer. It had an extensive hematoma between the wrist and the elbow of the right wing; however, fang marks were not apparent, possibly because of an extensive hemorrhage and a tear in the skin.

The likelihood that snakebite caused the death of the skimmer adult suggests the potential danger of western diamondbacks to adult waterbirds. King (Southwest. Nat. 20:416–417, 1975) observed a western diamondback attempting to swallow an adult Laughing Gull (*Larus atricilla*).

Effective defense of offspring against venomous predators may be difficult and costly to adults. On 5 May 1982 I began observations of a fenced colony of 61 nesting pairs of Caspian Terns at 13:30. The behavior of the terns became unusually agitated at 19:47 when an alarm call was given. The call given was a nonspecific one that increased the alertness of all adults in the colony. The first call was followed by many others as adults within a radius of about 5 m of the location of a rattlesnake flew up and hovered approximately 2 m over their nests, without diving at the snake. Adults between about 5 and 7 m from the snake remained standing on the ground in an alert posture, while those farther away simply looked in the direction of the disturbance and then resumed incubating or brooding. Parents may protect offspring that are especially vulnerable and have received substantial parental investment (Trivers, pp. 136–179 *in* Sexual Selection and the Descent of Man, 1871–1971, B. Campbell, ed., Aldine, Chicago, Illinois, 1972), if costs to the parents' own survival are small. Proximity to the initial alarm calling or to the snake, and presumably the specific attributes of this predator such as mobility or maneuverability, influenced the response of colony members.

Four min after I heard the initial alarm call, the snake moved from behind some vegetation into my sight, at which time I left the blind and killed the snake. It was refrigerated overnight, then frozen and later measured (snout–vent length = 0.94 m). Five Caspian Terns, aged 3 d or less, were found in its stomach. Chicks in the area of the intruding rattlesnake did not run, but crouched in the nest cup and remained still. This is the typical response of young Caspian Tern chicks to alarm calls (pers. obs.). Such behavior is more appropriate for defense from visually oriented predators and is apparently ineffective against rattlesnakes orienting to odors or heat (Klauber, Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind, Univ. California Press, Berkeley, California, 1972).

Western diamondbacks (1.25 m snout–vent length) take about 7–10 min to ingest a 35 g lab mouse (*Mus musculus*; S. Secor, pers. comm.). Newly hatched Caspian Tern chicks weigh about 70 g (Quinn, unpubl.). The advanced state of digestion of the first ingested chick (through the skin to the muscle layer) combined with the timing of the snake's activity in

the colony (3–4 min) may be evidence that the snake had eaten one or more chicks earlier in the day and had remained inactive, under cover, until observed.

I did not see adult birds attack the rattlesnake. Avoidance of venomous snakes by adult birds has been documented (Smith, Science 187:759–760, 1975; Caldwell and Rubinoff, Auk 100:195–198, 1983). Other intruders elicit flushing and are often relentlessly attacked by Caspian Terns (e.g., Herring Gulls [*L. argentatus*], Turkey Vultures [*Cathartes aura*], Great Blue Herons [*Ardea herodias*], and researchers [pers. obs.]). Mobbing of nonvenomous snakes has been reported in some species. Blem (Wilson Bull. 91:135–137, 1979) observed nesting Bank Swallows (*Riparia riparia*) mobbing black rat snakes (*Elaphe obsoleta*), but did not mention contact with the snake by the birds. Francesca Cuthbert (pers. comm.) noted Common Terns (*S. hirundo*) contact-mobbing common garter snakes (*Thamnophis sirtalis*), and in one case a snake was killed. In contrast, Fetterolf (Can. Field-Nat. 93:317–318, 1979) reported that adult Ring-billed Gulls (*L. delawarensis*) stood near their nests and displayed no anti-predator behavior while a common garter snake (*T. sirtalis*) ingested two gull chicks.

Responses to western diamondback rattlesnakes by adult Caspian Terns probably increased detectability of the snake for all colony members. Active defense of offspring, however, was not increased, nor was the response of offspring effective. Parents responded to the rattlesnake according to risks to themselves despite the vulnerability of their young. Hovering without attack may be a common response of colonial nesting birds reacting to potentially lethal terrestrial predators.

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Acorn Woodpecker mutilates nestling Red-breasted Sapsuckers.—On 22 June 1980 I observed an interaction between Acorn Woodpeckers (*Melanerpes formicivorus*) and nesting Red-breasted Sapsuckers (*Sphyrapicus ruber daggetti*) along Bear Valley Creek at the Bear Valley Headquarters of the Point Reyes National Seashore, Marin County, California. The Red-breasted Sapsuckers were nesting approximately 8 m up in a madrono (*Arbutus menziesii*) snag in a coast live oak (*Quercus agrifolia*), tanbark oak (*Lithocarpus densiflorus*), and California bay laurel (*Umbellularia californica*) woodland just upslope from a red alder (*Alnus rubra*) thicket bordering Bear Valley Creek. The nest tree was used to a limited degree as an acorn storage site by Acorn Woodpeckers. The nest at this location was unusual as the breeding range of Red-breasted Sapsucker has previously been reported in the northern Coast Range of California south only to the middle of Mendocino County (Grinnell and Miller, Pacific Coast Avifauna No. 27, 1944). More recent evidence indicates that it breeds regularly south to northern Sonoma County (Shuford, unpubl.), making the nesting at Bear Valley an isolated occurence even farther south.

I first observed an adult sapsucker approach the nest hole with food. The bird hitched up to the hole and poked its head inside several times, each time emerging with insects still in its bill. It then flew away with the food and I moved farther from the nest site. A sapsucker returned and I again witnessed a feeding attempt before the bird flew off. I then moved to a spot 20–25 m from the tree and concealed myself on the ground amidst vegetation where I felt the sapsucker(s) would be unable to detect my presence. Once more a sapsucker returned and repeated the previous two performances, again flying off with a bill full of food.

A male Acorn Woodpecker then flew onto the snag and went straight to a fresh irregular hole, about one-half the size of the sapsucker nest hole and approximately 90° around the side of the tree and about 15 cm below the entrance to the sapsucker nest hole, and began drilling at the edge of it. Once or twice during its three trips to the snag the sapsucker(s) had also hitched close to this irregular hole as if investigating it, although it never attempted to put its head inside. The Acorn Woodpecker pecked hard on the edge of the hole, then pecked inside and finally pulled something part of the way out that on closer scrutiny proved to be the wing of a nestling sapsucker. The woodpecker pecked vigorously and pulled at the wing, which began to bleed. After much pecking and pulling, the Acorn Woodpecker ripped off a piece of flesh approximately 2–3 cm long and flew off with it. About a minute later a male Acorn Woodpecker landed on the nest tree and was joined by another male that clung to the side of the tree while the first bird pecked at the protruding wing. They both soon flew off while the stubby wing was still in sight at the hole.

I waited about 20 min but left as no more activity occurred at the nest site. On my way back to the nest, near a spot along the creek the sapsuckers had frequented while foraging, I saw an adult sapsucker in flight pursuit of an Acorn Woodpecker. Howell (Condor 54: 237–282, 1952) also observed Red-breasted Sapsuckers on breeding territories chasing off other species of woodpeckers. I waited again for about 10 min near the snag for more activity but there was none. Minutes later J. Evens and I inspected the area below the nest tree and found many fresh, moist pin feathers that had already erupted from their sheaths. Further search revealed the freshly dead body of a nestling sapsucker, which was bleeding and mutilated about the wings (specimen #70758 at the California Academy of Sciences). At the time we found the dead nestling on the ground, the wing of the nestling that had been pecked at by the Acorn Woodpecker was still visible at the hole on the side of the nest cavity. Thus, at least two young sapsuckers were involved in this incident. Presumably the nestling on the ground was pulled out of the irregular hole by the Acorn Woodpecker. On 2 July, on the advice of L. Binford, I procured a ladder and climbed to the nest hole to investigate further, and found the nest cavity empty except for a few downy body feathers along with sawdust and woodchips lining the floor of the cavity.

In retrospect it is obvious why the sapsucker(s) kept emerging from the nest hole with insects still in its bill. The nestling sapsuckers were already dead, or at best in a very weakened condition at the time of my observations. At no time did I hear any of the incessant/insistent begging noises typical of nestling sapsuckers (Howell 1952). In addition, I heard no distress calls while the Acorn Woodpecker pecked at the nestling. The freshness of the dead nestling found at the base of the tree, together with the sighting of the bleeding youngster at the hole in the side of the nest cavity, and the repeated sightings of the adult sapsuckers carrying food in the direction of the nest tree on 21 June—the day before its exact location was discovered—support the idea that the young had died or were killed the morning I made my observations.

Why the Acorn Woodpecker first drilled at the edge of the smaller hole and then pulled on the sapsucker wing from this location when presumably it could have reached the young sapsuckers from the original nest entrance is unknown. As Howell (1952) found that sapsucker nest holes are exceptionally small, and that birds invariably have to struggle to enter

and leave, the somewhat larger Acorn Woodpecker may be physically excluded from such holes. Although the origin of the smaller, irregular hole is uncertain, it seems unlikely the adult sapsuckers would have initiated nesting in a cavity with a hole in the side that potential predators could get to. Presumably this irregular hole was drilled by the Acorn Woodpecker(s), perhaps after being chased from the nest entrance by the sapsuckers.

As Acorn Woodpeckers are known to chase heterospecifics away from their granaries, sapsucking trees, acorn-gathering trees, roosts, nest holes, anvils, and hawking perches (MacRoberts, Condor 72:196–204, 1970), proximity of the sapsucker nest hole and territory to the territory of the Acorn Woodpecker group presumably nesting nearby might have elicited aggressive behavior from the Acorn Woodpeckers. The sapsucker nest tree was an acorn storage tree of the Acorn Woodpeckers, and this alone may account for their aggression towards the sapsuckers.

Other instances of Acorn Woodpecker aggression against Red-breasted Sapsuckers have been recorded. Grinnell (Univ. Calif. Publ. Zool. No. 5:1–170, 1908) saw an Acorn Woodpecker drive a sapsucker away from its borings in an alder tree and then "go the rounds of the borings" drinking from each. D. DeSante (pers. comm.) saw an Acorn Woodpecker holding a Red-breasted Sapsucker on the ground and pecking it on 16 Dec. 1978 at Tomales Bay State Park, Marin County, California. Direct evidence of nest predation by Acorn Woodpeckers was observed by Bryant (Condor 23:33, 1921) who saw one perched on the nest and eating the egg of a Western Wood-Pewee (*Contopus sordidulus*). P. Henderson (pers. comm.) has observed an Acorn Woodpecker drilling on a nest box occupied by Tree Swallows (*Iridoprocne bicolor*) at his home in Guerneville, Sonoma County, California. He later found dead baby Tree Swallows under the nest box, though no direct evidence was found to implicate the Acorn Woodpeckers.

Acorn Woodpeckers commit acts of inter-specific as well as intra-specific aggression. In their communal breeding groups, female Acorn Woodpeckers will destroy other females' eggs (Mumme et al., Nature 306:583–584, 1983) and apparently also will kill other females' young in the nest (Stacey and Edwards, Auk 100:731–733, 1983).

Acorn Woodpeckers subsist largely on dried and green acorns, flycatching, sapsucking, and, less frequently, on fruit, bird eggs, and lizards (MacRoberts 1970). W. Koenig (pers. comm.) has seen them eat western fence lizards (*Sceloporus occidentalis*) on several occasions. Considering their occasional carnivorous habits it seems likely that Acorn Woodpeckers may rob nests of eggs or young when the opportunity arises. The closely related Red-headed Woodpecker (*Melanerpes erythrocephalus*) frequently preys on the eggs and young of other species of birds, and the Great Spotted Woodpecker (*Picoides major*) sometimes feeds on young birds (Short, Woodpeckers of the World, Delaware Mus. Nat. Hist. Monog. Ser. No. 4, 1982).

I thank J. G. Evens for discussion in the field and W. D. Koenig for helpful comments on an earlier draft of the manuscript. R. N. Conner, R. Mumme, and L. L. Short provided helpful comments on a later draft of the manuscript. Personnel of the Point Reyes National Seashore kindly provided a ladder and assistance in reaching the nest hole. This is contribution No. 275 of the Point Reyes Bird Observatory.—W. David Shuford, *Point Reyes Bird Observatory, 4990 State Route #1, Stinson Beach, California 94970.* *Accepted 7 Jan. 1985.*

Wilson Bull., 97(2), 1985, pp. 237–239

Timing of primary molt in first-year Golden-Plovers and some evolutionary implications.—Connors (Auk 100:607–620, 1983) presents a strong case for elevating the two subspecies of Lesser (American) Golden-Plovers (*Pluvialis dominica dominica* and *P. d. fulva*) to full species *P. dominica* and *P. fulva.* Based upon a discriminant function analysis involving various measurements and plumage characteristics, Connors found that phenotypically intermediate specimens were no more frequent in areas of sympatry than in areas of allopatry. He proposed that hybrids are at a selective disadvantage relative to the conditions imposed by the very different migration routes and wintering areas of the two taxa (*dominica* winters on grasslands of South America; *fulva* on islands and atolls of the Pacific); thus, "the requirements of migration and winter range drive the process of speciation." Here, I report observations on the timing of primary molt in first-year golden–plovers that reveal a major difference between *dominica* and *fulva.* This adds yet another distinction between the two forms.

Johnson and Johnson (Condor 85:406–419, 1983) analyzed molts in *fulva* using specimens from Oahu, Hawaii (N = 70 banded and 83 collected) and Enewetak Atoll, Marshall Islands (N = 84 collected). Specific findings relevant to this paper are: (1) The juvenal primaries are not molted during the first winter; consequently these feathers become faded and worn by spring. (2) On Oahu, some first-year birds migrate (using the worn juvenal primaries), while others remain on the wintering grounds and "over-summer." Many (possibly all) young birds over-summer at Enewetak. Over-summering individuals begin molting juvenal primaries during the summer; migratory first-year birds defer this molt until they return to the wintering grounds in the fall, having made two southward and one northward migration with the same primaries. (3) The cloacal bursa remains large enough to be a definitive criterion of age in almost every individual through the first spring and into the second summer of life. Most individuals finally lose the bursa at about one year of age. (4) Adults molt their primaries on the wintering grounds; the new feathers appear dark and fresh in the spring and contrast strikingly with the worn juvenal primaries of first-year birds at that season.

Migrating *dominica* are relatively common near Moorhead, Minnesota, in the spring, and I collected 16 specimens during the periods 13–15 May 1971 and 4–14 May 1974. Six of these contained cloacal bursae that were identical in appearance and weight (ranging from 18 to 124 mg) to the springtime bursae of first-year *fulva.* Assuming that the chronology of bursa development is the same in both taxa, the six *dominica* with bursae were first-year birds. All *dominica* specimens, including those with bursae, had fresh, dark primaries like those of adult *fulva* in the spring. If the timing of primary molt in first-year *dominica* is similar to that of *fulva,* I should have found worn primaries in those birds with bursae. Though the sample is limited, it is reasonable to conclude that juvenal *dominica* molt their primaries during the first winter of life.

Additional study might reveal at least some variation from the foregoing pattern as it is not uncommon for primary molt schedules in first-year shorebirds to vary from one region of the winter range to another (Prater et al., Guide to the Identification and Ageing of Holarctic Waders, British Trust for Ornithology, Field Guide 17, 1977; Myers et al., Going to Extremes: Why Do Sanderlings Migrate to the Neotropics? Ornithol. Monogr., No. 36, 1985). However, Connors' (1983) findings further suggest that primary molt in the first winter is the typical pattern for *dominica.* He classified primary wear and appearance among birds collected in spring migration or on breeding grounds as follows: many *fulva* (about 30%) with moderate to heavy wear, the remainder with light wear to fresh; almost all *dominica* (about 95%) with light wear to fresh, a few with moderate wear, none with heavy

wear. Based on the assumption that first-year birds have worn primaries (valid in *fulva,* Johnson and Johnson 1983), Connors interpreted his results as indicating that "many more *fulva* than *dominica* return to breeding grounds during their first spring." Another possibility is that *dominica* molts the juvenal primaries earlier than *fulva,* and that many of the *dominica* specimens examined by Connors were first-year birds. The latter interpretation is consistent with the findings presented here and with observations on the winter range. Wetmore (Observations on the Birds of Argentina, Paraguay, Uruguay, and Chile, U.S. Natl. Mus. Bull. No. 133, 1926) noted only a few *dominica* over-summering in Argentina and implied that such scattered individuals were unusual. I have found no subsequent reports contradicting Wetmore's findings, and no records suggesting that *dominica* characteristically over-summers in areas between the winter and summer ranges. Thus, I concur with Stresemann and Stresemann (Die Mauser der Vögel, J. Ornithol. 107, Suppl., 1966) that first-year *dominica* typically return to the breeding grounds.

One can only speculate as to the evolutionary basis of the difference between *fulva* and *dominica* in the timing of juvenal primary molt. One possibility is that resource availability differed significantly on the respective wintering grounds of these taxa during the speciation process. Until relatively recent times, most of the insular Pacific was forested and low upland cover suited to foraging by plovers was lacking. Under these conditions, wintering *fulva* must have been concentrated on intertidal and occasional marshland habitats, which perhaps offer less food than upland grasslands. Thus, *fulva* may have evolved in an environment with limited capacity to sustain the energy costs of molting whereas the pattern may have been the reverse for *dominica.* In *fulva,* resource availability would be a particular problem for juveniles arriving for the first time on the wintering grounds (juveniles arrive about six weeks later in fall migration than adults, Johnson and Johnson 1983) as they would be confronted with the difficulty of establishing themselves on a limited range already occupied by older birds. Survival in the first winter may require that birds defer wing molt so as to commit their energy resources to matters of more immediate importance. That the timing of primary molt in first-year birds may be related fundamentally to winter resources is implicit in studies of the Sanderling (*Calidris alba*) by Myers et al. (1985). They found that first-year birds wintering in Chile replaced their primaries while birds wintering in California did not. While emphasizing the need for more research, the authors concluded that "resource conditions for Sanderling appear to be more favorable on Chile's northern coast than in California." If this overall scenario is accurate, hybrid individuals on the winter range of *fulva* that attempted to molt might lack critical resources and could be less likely to survive. The fate of hybrids on the winter range of *dominica* is less clear. From the perspective of resource availability, such birds might be more likely to survive. The timing of their molt, however, may be out of synchrony with that of *dominica,* and this and/or other features peculiar to hybrids might result eventually in a selective disadvantage.

Large areas of Hawaii have undergone development compatible with the requirements of wintering plovers (i.e., land converted to lawns, pastures, agricultural fields, airports, etc.). Most of these changes are relatively recent and seem beneficial as birds can now forage on previously unavailable uplands rich in insect prey. Johnson and Johnson (1983) found among first-year birds wintering in Hawaii that some became fat and acquired alternate body feathering, while others remained lean and drab. The fatter, more brightly colored birds migrated; the others over-summered.

Much of the insular Central and South Pacific appears to offer less food and space suitable for plovers than comparable areas in Hawaii. Such restrictions combined with long migratory flights and competition with older, more experienced birds (our studies in Hawaii show the latter to be remarkably site-faithful and potentially long-lived) could result in stressful wintering conditions for most young birds. Insufficient winter resources would preclude

primary molt, gonadal maturation, premigratory fattening, and migration, thus culminating in over-summering behavior. As the molting of juvenal primaries is not prerequisite to spring migration (at least not at the northern end of the winter range in Hawaii), lack of molt cannot be coupled with over-summering in a cause-effect relationship. Rather, both phenomena appear to be adaptations that enhance survival in the first winter. I suggest that over-summering behavior represents the ancestral condition for *fulva* throughout the Pacific, that it is presently the norm on ranges south of Hawaii, and that the variability encountered in Hawaii reflects a recent improvement in the food supply.

There are as yet no data to support my proposed scenarios of an easier life on the pampas as compared to the Pacific, and on improved habitats in Hawaii relative to other regions of the Pacific. The critical factor is the relative availability of resources on a per capita basis. Comparative studies of golden-plovers on their Pacific and South American wintering grounds offer a potentially fruitful opportunity to evaluate Connors' (1983) hypothesis that conditions on the winter range are fundamental to speciation, and to consider further the questions that I have raised here. Information is needed concerning densities of wintering birds, availability and dependability of food supplies, competition for food, foraging success, body weights, and time-activity budgets; with particular attention given to the biology of first-winter individuals.

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Wilson Bull., 97(2), 1985, pp. 239–240

Wing molt by a nesting Pied-billed Grebe.—Although there are exceptions, molting and breeding of birds typically occur at separate times during the annual cycle. These events are thought to be energetically incompatible in most species (Payne, pp. 103–155 *in* Avian Biology, Vol. 2, D. S. Farner and J. R. King, eds., Academic Press, New York, New York, 1972). According to Palmer (Handbook of North American Birds, Vol. 1, Yale Univ. Press, New Haven, Connecticut, 1962), the postnuptial molt of Pied-billed Grebes (*Podilymbus podiceps*) occurs in autumn; however, there is much individual variation in the timing and duration of this molt. Flight feathers are all shed and replaced before any apparent loss of other feathers. Prior to this note, molting by nesting Pied-billed Grebes has not been reported.

After finding shed flight feathers on the surfaces of several active Pied-billed Grebe nests on Rush Lake, Winnebago Co., Wisconsin (43°56′N, 88°48′W), we suspected that at least some individuals of this species were molting while nesting. Our suspicions were confirmed on 7 July 1980. We placed an automatic nest-trap (Otto, N. Am. Bird Bander, 8:52–53, 1983) on an active Pied-billed Grebe nest on which we found several shed flight feathers. The nest contained a six-egg clutch that had been completed on approximately 25 June. This was a rather late-season nest for Pied-billed Grebes on Rush Lake (Otto, M.S. thesis, Univ. Wisconsin–Oshkosh, Oshkosh, Wisconsin, 1983). We captured an adult Pied-billed Grebe that was undergoing wing molt. All old primaries and secondaries had been shed, and there was nearly 1 cm new growth of the most distal primary of each wing. We found

no evidence of body molt. The weight of the bird (416 g) indicated that it was probably a female. (Weights of adult Pied-billed Grebes from Palmer [1962], and Norris and Johnston [Wilson Bull. 70:114–129, 1958] show females ≤435 g, males ≥435 g.) We released the grebe after banding it (U.S.F.W.S. aluminum band 645-30146). Twenty-seven other nesting Pied-billed Grebes that we examined on Rush Lake during 1979 and 1980 showed no signs of molting. These birds included 15 suspected females and 12 suspected males captured between 14 May and 18 July. Our trapping attempts were confined to the days after the completion of the clutch but prior to the start of hatching.

Because the flight feathers constitute a relatively small portion of the plumage, replacement of these feathers should require much less energy than would a complete molt. If molting of the flight feathers is energetically compatible with the nesting activities of Pied-billed Grebes, we suggest that the nesting season is an opportune time for these birds to replace their flight feathers; nesting Pied-billed Grebes rarely fly (pers. obs.), and they have rather small home ranges. Glover (Wilson Bull. 65:32–39, 1953) estimates the average home range of nesting Pied-billed Grebes to be less than 2 ha. Grebes could easily traverse such a small area by swimming. Therefore, flightlessness owing to wing molt should be of negligible consequence to nesting Pied-billed Grebes. More information will be needed to determine if molting of flight feathers by nesting Pied-billed Grebes reduces either the production of fledglings or the survival of molting adults. Five of the six eggs hatched in the nest on which we captured the molting grebe. We do not know the fates of the hatchlings or the molting adult.

Our observations indicate that wing molt does occur, albeit uncommonly, among nesting Pied-billed Grebes. Munro (Studies of Waterfowl in British Columbia: the Grebes, Occas. Paper Br. Col. Prov. Mus. No. 3, 1941) presents an additional report of molting by nesting grebes. He found both members of a nesting pair of Horned Grebes (*Podiceps auritus*) partly molted to the winter plumage on 10 August. This was the latest date for a Horned Grebe nest with eggs for Munro's study. We suggest that molting by nesting grebes is likely limited to late nesting individuals.

Acknowledgments.—R. C. Banks and K. C. Parkes provided helpful comments on an earlier version of this manuscript.—James E. Otto, *1108 Bay Shore Dr., Oshkosh, Wisconsin 54901*; and David L. Strohmeyer, *Dept. Biology, Univ. Wisconsin–Oshkosh, Oshkosh, Wisconsin 54901.* *Accepted 23 Oct. 1985.*

Wilson Bull., 97(2), 1985, pp. 240–241

Partition of water loss from the eggs of the Sooty Tern between the pre-pipping and pipped periods.—In a previous publication (Rahn et al., Physiol. Zool. 49:245–259, 1976), it was reported that the total water loss from the eggs of the Sooty Tern (*Sterna fuscata*) over the entire incubation period amounted to 15% of the mass of the freshly laid eggs. More recent work on the White Tern (*Gygis alba*) and the Gray-backed Tern (*Sterna lunata*) implies that the figure of 15% is an underestimate of the true water loss because the augmented water loss from pipped eggs was not measured in the earlier study (Pettit et al., Condor 84: 355–361, 1981; Whittow et al., Condor, in press, 1985). The purpose of the study reported here was to measure the water loss from pipped eggs of the Sooty Tern.

The site of the study was Green Island, Kure Atoll (28°25′N, 178°10′W) in the Northwestern Hawaiian Islands. The water loss from the eggs was determined by measuring the

TABLE 1

WATER LOSS FROM PIPPED AND UNPIPPED EGGS, TOGETHER WITH THE DURATION OF THE PIPPED AND UNPIPPED PHASES OF INCUBATION, IN THE SOOTY TERN. SD = STANDARD DEVIATION; N = NUMBER OF MEASUREMENTS

Phase of incubation	Mean duration (hr)	Mean daily water loss (mg/day ± SD)	N	Water loss during phase in mg (% of total)
Unpipped	577[a]	162.21 ± 28.68	36	3900 (59.0)
Star-fracture	78[a]	437.91 ± 139.25	14	1423 (21.5)
Star-fracture–pip-hole[b]	—	604.31 ± 100.81	7	— —
Pip-hole	31[a]	995.66 ± 281.21	4	1286 (19.5)
Total	686[a]			6609 (100)

[a] Brown, Condor 79:133–136, 1977.

[b] The eggs were star-fractured when they were first weighed and there was a distinct pip-hole at the time of the second weighing.

mass loss (Rahn and Ar, Condor 76:147–152, 1974) using an Ohaus field balance (Model 1010-10).

The mean dimensions of 33 eggs were: length = 51.1 mm ± 1.9 (SD); width = 35.7 mm ± 1.2 The mean daily water loss from the eggs was least in unpipped eggs and greatest in eggs with pip-holes (Table 1). The mean incubation period of the Sooty Tern on Manana Island, in the main Hawaiian Islands, is 686 h (Brown, Condor 79:133–136, 1977). The initial star-fracture of the shell occurs 109 h prior to hatching, and a pip-hole is formed 31 h before hatching. Using these data in conjunction with the measurements of water loss made in the present investigation, it is apparent (Table 1) that the mean total water loss from the eggs over the entire incubation period is 6609 mg. This represents 18.5% of the mass of the freshly laid egg (Rahn et al. 1976), which is higher than the 15% value reported by Rahn et al. (1976). The mean daily water loss from unpipped eggs was 14.6% lower than that reported by Rahn et al. (1976), raising the possibility that the conditions during incubation were somewhat different. This notwithstanding, the water loss from pipped eggs (initial star-fracture to hatching) is 2709 mg (1423 + 1286, Table 1), which represents 41.0% of the water loss from the egg over the entire incubation period, although the time interval between star-fracture and hatching amounts to only 15.9% of the incubation period.

The results of the present study, together with those of three earlier investigations (Pettit et al. 1981, Whittow et al. 1984, Pettit and Whittow 1984), reveal that the total water loss from the eggs of tropical terns and noddies is a greater percentage of the mass of the freshly laid egg than had hitherto been reported (Rahn et al. 1976), and that the water loss from pipped eggs represents a disproportionate fraction of the total water loss from the egg.

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G. C. WHITTOW, *Dept. of Physiology, John A. Burns School of Medicine, Univ. Hawaii, Honolulu, Hawaii 96822.* *Accepted 5 Jan. 1985.*

Wilson Bull., 97(2), 1985, pp. 242–243

Determining whether Common Loon eggs have hatched.—Egg remains may be found in nests of many nidifugous species after the eggs have hatched (Wallace, An Introduction to Ornithology, The Macmillan Co., New York, New York, 1963), presumably because there is no selective advantage in removing them, as the young leave the nest so soon. Palmer (Handbook of North American Birds, Vol. 1, Yale Univ. Press, New Haven, Connecticut, 1962), however, states that Common Loons (*Gavia immer*) sometimes carry away shells and membranes. Common Loons brood the first chick on and off the nest until the second chick hatches, whereupon the family leaves the nest and does not return. The danger of nest predation would be enhanced before the hatching of the second egg if the remains of the first egg were left on the nest, because the egg membranes and the inner surface of eggshells do not have the cryptic coloration of newly hatched young or of the outer shell surface. It would therefore be advantageous for the parents to remove the remains of the first egg unless the two hatched more or less synchronously. This may help to explain why the remains of only one egg are often found even when two eggs are known to have hatched (McIntyre, Ph.D. diss., Univ. Minnesota, Minneapolis, Minnesota, 1975).

Researchers conducting surveys of breeding loons often need to know which nests have had eggs that hatched. Although Heimberger et al. (Wilson Bull. 95:431–439, 1983) stated that they used the presence of egg membranes on loon nests to confirm hatching, this method has not been reported elsewhere. Here, I present data suggesting that the presence of an egg membrane sac can be used to confirm hatching.

While studying loon breeding success on 29 lakes in the vicinity of Sudbury, Ontario, in 1982 and 1983, I examined the egg remains of 46 loon nests. Each lake had only one pair of loons, so there was no difficulty in matching loon chicks with their nests. One or two egg membrane sacs were found in 17 of the 46 nests (37%; Table 1). Each sac had a large hole through which the chick had emerged. One or two loon chicks were observed in 13 (76%) of these cases. I believe that eggs in the remaining four nests also hatched, but that the young died before I could observe them. Loon chicks are especially vulnerable to hypothermia and fatigue during the first 2 weeks after hatching (Olson and Marshall, Minn. Mus. Nat. Hist., Occ. Paper 5:1–77, 1952). Also, one of the nests was disheveled, suggesting predation. It is possible that in this case the chick and the second egg were taken before the latter hatched.

In the other 29 cases, no egg membrane sac was found; instead, pieces of egg membrane were found still attached to their respective shell fragments. One or two young were observed in 14 (48%) of these cases, while in the other 15 cases no young were observed, suggesting

TABLE 1

NUMBER OF EGG MEMBRANE SACS IN EACH NEST AND NUMBER OF CHICKS OBSERVED ON EACH LAKE FOR 46 NESTS

Number of chicks observed	Number of egg membrane sacs on the nest		
	0	1	2
0	15	2	2
1	8	6	0
2	6	3	4

that the contents of the latter nests had been depredated. The absence of an egg membrane sac therefore does not help in distinguishing successful nests from depredated ones. However, sac presence can be used to verify hatching with reasonable certainty.

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Wilson Bull., 97(2), 1985, pp. 243–244

Eastward range expansion of the Marbled Godwit in South America.—On 20 February 1984, we saw 7 Marbled Godwits (*Limosa fedoa*) on a mud flat of the Bocaripo Lagoon that forms part of the Chacopata Lagoon complex on the north side of the Araya Peninsula (10°41′N, 63°46′W), state of Sucre, in northeastern Venezuela. The birds were feeding intensely and were not disturbed by our approach; we observed them for about half an hour through 8× binoculars and a 15–60× zoom telescope from a distance of less than 40 m, and checked the distinctive field marks of their winter plumage. Between 2 and 7 individuals were regularly sighted at the same location by the third author from 21 July to mid-Oct. 1984, and photographic records were taken by her and Luis Gerardo Gonzalez. The species was also identified in the same area by Gedio Marin and the second author on 28 Jan. 1983, and had previously been observed on 3 occasions (Jan., 26 Mar. and 5 Apr. 1982) by Gedio Marin and Roberto Egañez or the second author in El Peñón Lagoon, approximately 3 km east of Cumaná, state of Sucre.

According to the A.O.U. Check-list (Check-list of North American Birds, sixth ed., American Ornithologists' Union, Lawrence, Kansas, 1983) and Meyer de Schauensee (Guide to the Birds of South America, Pan American Section of the International Council for Bird Preservation, Intercollegiate Press, 1982), *L. fedoa* is known to winter irregularly or locally south of Mexico on both coasts of Middle America, and in South America south to Chile on the Pacific coast. Blake (Manual of Neotropical Birds, Vol. 1, Univ. Chicago Press, Chicago, Illinois, 1977) and Meyer de Schauensee and Mack (pp. 429–463 *in* Meyer de Schauensee 1982) report sight records from northeastern Colombia on the Atlantic coast. Bond (Birds of the West Indies, Collins, London, England, 1979) and Blake (1977) consider *L. fedoa* as rare or casual in the West Indies. According to Bond (1979), the Marbled Godwit has been "recorded from Cuba, Jamaica, Hispaniola, Puerto Rico, St. Croix, Anegada, Grenada and Carriacou," and "questionably from Guadeloupe and Martinique." The species is listed by Meyer de Schauensee (1982) as occurring in Trinidad and Tobago. ffrench (A Guide to the Birds of Trinidad and Tobago, Livingston Publ. Co., Wynnewood, Pennsylvania, 1973) mentions it as "formerly recorded as a passage migrant, occurring on the coasts of Trinidad from August to October," but questions the reports for Tobago by James Kirk in 1883. The A.O.U. Check-list (1983) considers as questionable the reports from the Lesser Antilles, Tobago, and Trinidad. Meyer de Schauensee and Phelps (A Guide to the Birds of Venezuela, Princeton Univ. Press, Princeton, New Jersey, 1978) do not mention the Marbled Godwit as occurring in Venezuela.

As far as we know, the present photographic evidence and sightings represent an expansion of the known winter range (casual) of the Marbled Godwit from the Pacific coast of South America eastward to the Caribbean coast of northeastern Venezuela. One copy of the color photograph has been deposited in the Colección Ornitologica Phelps in Caracas, and one is in the Ornithological collection, Department of Biological Sciences, University of Montreal.

Acknowledgments.—We thank Roberto Egañez, Luis Gerardo Gonzalez, and Gedio Marin for providing information from their field books. This note is a byproduct of ecological research supported by the Natural Sciences and Engineering Research Council of Canada, the Quebec Dept. International Affairs, the Univ. Montreal, and the Univ. Oriente.—RAYMOND MCNEIL, *Centre de recherches écologiques de Montréal and Dépt. Sciences biologiques, Univ. Montréal, C. P. 6128, Succ. A, Montréal, Québec H3C 3J7, Canada;* JOSÉ RAMÓN RODRIGUEZ S., *Dept. Biología, Univ. Oriente, Cumaná, Sucre, Venezuela;* AND FRANCINE MERCIER, *Dépt. Sciences biologiques, Univ. Montréal, C. P. 6128, Succ. A, Montréal, Québec H3C 3J7, Canada.* *Accepted 16 Nov. 1984.*

Wilson Bull., 97(2), 1985, p. 244

A record of extreme leucism in the Carolina Wren.—In Westport Point, Bristol County, Massachusetts, I observed an all white Carolina Wren (*Thryothorus ludovicianus*) on 21 Aug. 1984. The bird was in the company of other Carolina Wrens (possibly a family group) in an area of undergrowth in a mixed-hardwood forested hillside. The bird apparently had fledged recently as it was still being fed by an adult (of normal plumage) that foraged with it in the understory. The bird was totally white (except for brown eyes), with no noticeable trace of brown or any other color in its plumage. It was seen by two other observers at the same time (N. and C. McGrath) and by another local observer (K. Preston) later the same week.

This sighting is of interest in view of the fact that a literature review indicates that albinism is extremely rare in wrens. (Technically, because of the brown eye color this appears to be a case of extreme leucism, rather than albinism.) Ross (Cassinia 47:2–21, 1963) reports only one record for the Carolina Wren, and that bird had only a trace of white on the outer edge of each wing and on both sides of the lower neck. Terres (p. 1029, The Audubon Society Encylopaedia of North American Birds, Alfred Knopf., New York, New York, 1980) lists a second record of a partial albino Carolina Wren for a bird banded in December 1959, in Maryland.—JOSEPH J. SENECA, *Dept. Economics, Rutgers Univ., New Brunswick, New Jersey 08903.* *Accepted 15 Dec. 1984.*

Wilson Bull., 97(2), 1985, pp. 245–258

ORNITHOLOGICAL LITERATURE

IDENTIFICATION GUIDE TO EUROPEAN PASSERINES, 3rd revised and enlarged edition. By Lars Svensson. Published by the author, Stockholm, Sweden, 1984:312 pp., illus., 10.5 × 18.5 cm. Order from author (Sturegatan 60, S–114 36 Stockholm, Sweden, SCr. 120 or $15.00 US [cash]) or from British Trust for Ornithology, Beech Grove, Tring, Herts HP23 5 NR, U.K., £9.00.—A short review of the 2nd (1975) edition of this book was published by Lloyd-Evans (Wilson Bull. 89:190–191, 1977); the 1st (1970) was never reviewed in this journal. The author himself states "The number of new species (29) and subspecies (about 20), as well as the numerous new characters, illustrated by about 150 new drawings [added to ca. 160 in the 2nd ed.], makes this third revised edition almost a new book." With that in mind, and because there are comments applicable to both the 2nd and 3rd editions that were not made by Lloyd-Evans, I will review this work in somewhat greater detail than is usual for a new edition.

In addition to the revisions mentioned by the author (see above), a major change in this edition is the adoption of the classification, sequence, and nomenclature of Voous (List of Recent Holarctic Bird Species, 1977), replacing those of Vaurie (The Birds of the Palearctic Fauna, Vol. 1, 1959).

The book begins with a chapter on "Directions for use," including sections on numbering of remiges, wing-formula, measurements, colors, and references (i.e., a short introduction to the bibliographies at the end of the book). Lloyd-Evans was critical of Svensson's numbering of the primary feathers ascendantly (from the wing tip toward the body), pointing out that "most modern molt studies employ the descendant order, i.e., that in which the feathers are usually replaced." An equally important argument for the descendant numbering of primaries is based on homology. The outermost primary of a nine-primaried bird is homologous with the second-outermost of a ten-primaried bird, and this is self-evident when their outermost primaries are numbered 9 and 10 using the descendant system; Svensson calls both of the non-homologous outermost primaries number 1.

In the section on measurements, the author describes three techniques for measuring wings: unflattened (chord), flattened, and maximum length (flattened and straightened). He used the second of these in his previous editions, but has now adopted the third, remeasuring practically all wing-lengths in the book. He reproduces a table showing pairwise comparisons, both in mm and percent, of measurements for the same series of birds, both living and specimens, taken by these three techniques. I have had students test techniques of wing measurement as a laboratory exercise, and invariably the maximum length method gives the most consistent and reproducible results using study skins. Svensson recommends this technique for banders handling live birds, stating that it has been adopted by the British Trust for Ornithology and other European ringing schemes. It is unfortunate that few, if any, of the North American banding stations employ this wing measurement technique, as such stations as Manomet and Powdermill have accumulated such tremendous numbers of measurements in their files as to make it impractical to change to another system, even though it is clearly more accurate.

In the discussion of bill measurements, Svensson fails to mention the now widely used distance from the bill tip to the anterior (i.e., distal) edge of the nostril, although he cites such measurements from the literature at least once (*Chersophilus duponti*, p. 45). He instructs the reader to avoid the use of dividers when measuring bills, although he does not say why, recommending slide calipers. I find slide calipers decidedly awkward to use, especially with small birds, and just as likely to injure a squirming bird as are dividers. (I assume this is the author's reason for condemning dividers.)

The discussion of colors and color terminology is brief but useful; the author recommends Smithe's "Naturalist's Color Guide" (1975, 1981).

The chapter on "General techniques for ageing and sexing" is, in general, quite thorough, and could be read to advantage by most American banders, although it appears that some techniques may not be equally applicable to New and Old World passerines. I will comment here on some specific techniques.

I am skeptical about the value of the presence or absence of hooked bill-tips as an age character (adults with bill hooks, juveniles without). If the bird is young enough not to have a fully grown bill, there are virtually always other characters by which the juvenile age class can be recognized. Bill tips of adult birds are constantly subject to both wear and breakage, often just an inconspicuous mm or two, whereas the fully grown bill of a young bird is likely to show the species-specific hooked tip in its pristine state, thus giving the reverse of the aging character suggested by Svensson.

Rectrix shape, and especially width, is apparently more useful for ageing New World than Old World passerines. Svensson states that "In *a few* species of those which retain some or all juvenile rectrices in their first winter plumage, the difference *in shape* of the rectrices is helpful when ageing." Thumbing through the book's illustrations suggests that this technique can be used for more than just "*a few*" species, although the author cautions that "to be on the safe side *the method should not be used alone.*" In some groups of New World birds, notably the Icterinae, the difference in rectrix shape between first-year and older birds can be downright dramatic.

Ageing birds using the pattern of growth bars ("fault bars") on the rectrices is probably more generally useful than Svensson indicates, although this technique, too, should be used in conjunction with other characters whenever possible. I doubt that any adult North American oscine normally molts the rectrices simultaneously (although the accelerated rectrix molt approaches simultaneity in a few, such as "*Cassidix*"). Svensson claims that the whole tail is molted "more or less simultaneously . . . normally or at least in many individuals" in 14 Palearctic species plus many *Locustella* and *Acrocephalus* species, and has "no doubt that it occurs in many other species." He lists *Calcarius lapponicus* and *Plectrophenax nivalis* among his 14 species, but in 13 specimens of the former and 6 of the latter in Carnegie Museum of Natural History (all adults in active tail molt) rectrix growth is clearly centrifugal. Although the replacement was accelerated in two of the Snow Buntings, any growth bars in the tails of these birds would *not* have been in identical positions across all rectrices.

Svensson does not mention iris color in his chapter on ageing techniques, although it is given in the text for *Prunella modularis, Sylvia curruca, Parus cristatus,* and perhaps a few others that I missed. Careful comparisons by bird banders in Europe would almost certainly reveal many more species in which iris color is a useful character, as it is in many American species.

It is hardly surprising that I quickly noted Svensson's failure to so much as mention the Humphrey-Parkes terminology for plumages and molts. Although he may prefer not to use it himself, his complete omission of this terminology from the text and of the Humphrey and Parkes papers from the molt bibliography was unwarranted, as the terminology has been so widely accepted on both sides of the Atlantic (and even translated into Dutch in the journal Dutch Birding!). For the two molts in the annual cycle of many passerines, Svensson selects the names "summer moult" and "winter moult," coded S and W in his elaborate system of abbreviations. This was an infelicitous choice, as many adult passerines molt in September or October (hardly "summer" in northern Europe!), and some species may be undergoing the prebasic molt as late as November; the author himself points this out for *Cisticola juncidis,* using quotation marks around "summer moult." Similarly, the "winter moult" of some species may extend into March or April.

In the individual accounts, diagnostic characters are given to separate each species, followed (where approriate) by discussions of subspecies known or likely to occur in Europe. The types of molt or molts exhibited by adults and young follow, after which there is a variable, often extensive discussion of age and sex characters, usually by season. For many species there are admirably clear line drawings by the author illustrating the character states described. However, as already noted by Lloyd-Evans, the many symbols and abbreviations used in the drawings and the text will need careful study, although I suspect that with a few weeks of actual practice at a banding station, these, like so many initially alien and baffling devices, would become second nature.

As virtually admitted by the author himself, his referencing system is unnecesarily time-consuming to use. There are four separate bibliographies: General Works & Handbooks; Taxonomy, Morphology & Variation; Moult; and General techniques for ageing and sexing: Methods. Unfortunately, the references at the end of the species accounts fail to direct the reader to the proper bibliography. Under *Sitta neumayer,* for example, the only reference is to Banks (1978), which turns out to be listed in the "Moult" bibliography, whereas the reference at the end of the next species accout, *Tichodroma muraria,* is found under "Taxonomy, Morphology & Variation."

Although I have been critical of a number of aspects of this publication, I am nevertheless fully appreciative of the tremendous amount of work involved in its compilation, both from the literature and from Svensson's own studies at museums and ringing stations. Although individuals such as Merrill Wood and institutions such as the Bird-Banding Office have produced or are producing partial guides to identifying, ageing, and sexing North American passerines in the hand, we have as yet nothing anywhere near comparable in both completeness and compactness to Svensson's book. The compactness, in fact, may be overdone. At banding stations of my acquaintance, birds are not processed in the field but in some sort of building, where equipment and a reference library are housed. Had Svensson used a larger page size instead of the pocket format of the present edition, he might well have been able to abandon some of his frustrating abbreviations. In any case, North American banders (whose identification problems with *Empidonax* pale in comparison to many of the Old World warblers) have good reason to be envious of their European colleagues.—Kenneth C. Parkes.

A Catalogue of the Ellis Collection of Ornithological Books in the University of Kansas Libraries. Volume 2, C–D. Compiled by Robert M. Mengel, edited by Alexandra Mason and James Helyar. Univ. Kansas Publ. Library Ser., 48, Lawrence, Kansas, 1983: 176 pp. $25.00.—The year 1972 saw the publication of the first volume of the catalogue of the Ellis Collection, perhaps the largest assemblage of ornithological books in North America. Here at last is the second installment. Because Volume 1 was not reviewed in these pages I shall comment on the entire undertaking (Volume 1 covers the letters A and B [xxix + 259 pp.] and is still available for $10.00).

Ralph Ellis developed ornithological bibliomania to a level not yet surpassed. Between 1935 and 1945 he acquired ornithological books at the rate of nearly 2000 per year to add to the 5000 already in his library. Thus, the Ellis Collection contains over 25,000 volumes, almost completely on birds. Ellis collected mostly through dealers in Europe and the US, purchasing, where possible, entire libraries (such as those of E. C. Stuart Baker and C. Hart Merriam), but he also traded with a few select individuals. A discriminating as well as ardent collector, he missed very few important works (among them Audubon's double elephant "Birds of America") and would certainly have missed fewer had his collecting not been cut short by his untimely death in December 1945 at the age of 37.

Through the efforts of E. Raymond Hall, director of the Museum of Natural History, Ellis

had agreed to donate his library to the University of Kansas, and at his death the books were transferred to the University to await cataloguing and description. Fortunately, Robert M. Mengel, a trained ornithologist, was able to start the task; his persistence and scholarship are clearly evident in the pages of the catalogue.

The Ellis catalogue is the latest in a series of detailed bibliographical descriptions of important ornithological libraries (among the others are those of Zimmer, Field Mus. Nat. Hist. Zool. Ser., Vol. 16, 1926; Wood, An Introduction to the Literature of Vertebrate Zoology, Oxford Univ. Press, London, England 1931; Anker, Bird Books and Bird Art, Levin and Munksgaard, Copenhagen, Denmark, 1938). Considerable duplication would be expected in these compendia, but the production of printed works was far less uniform in the past and many titles exist in a multiplicity of versions and collations (often being issued in pairs). Some are so complicated (e.g., Darwin's "Origin of the Species") as to require entire volumes to disentangle the bibliographic information. The result is that the catalogues tend to complement one another, each library having slightly (or considerably!) different versions of a given work. One strength of the Ellis Collection is the presence not only of multiple copies of many works but also of multipart works in original wrappers as issued. The latter are invaluable in establishing the actual publication date of each portion of the work, information of interest not only to bibliographers and historians but also to systematists.

The scope of the catalogue "includes all books with appreciable ornithological content which were acquired by Ralph Ellis as well as those bird books published before Ellis' death . . . which have been added to the collection by the University Libraries." The catalogue does not list serial or periodical titles nor most citations from the periodical literature. However, monographic works on geographic areas ". . . exceeding 75 pages, and complete in themselves" that were issued as volumes or parts of serials or periodicals have been included. Each title (single volume title or multivolume set) is numbered and listed separately. Entries are arranged alphabetically by first author (cross indexing will ultimately be provided in an index) and chronologically within author. Mengel has adhered strictly to the use of the actual author of the title being described (as opposed to an editor or the author of a larger work in which the ornithological part occurs) and thus occasionally differs in alphabetic sequence, from, for example, Zimmer (1926). For a few works lacking attributable authorship (e.g., dictionaries), the title is used for alphabetization. In cases of committee authorship (e.g., AOU check-lists) the name of the organization is used.

Each entry contains the following information: (1) Date (or range of dates) of publication. (2) Title: The text of the title page(s) is transcribed verbatim except for long lists of honors and the like, which are abbreviated in brackets. For multivolume treatises with complex titles, each title is described. (3) Collation: Included is the physical description of the book and its contents: dimensions, numbers of pages, and plates (including misprints and renumberings of plates, etc.), and technical descriptions of the signatures. Also included, where necessary, is a description (sometimes lengthy) of irregularities and variants, including comparisons with copies located elsewhere. (4) Content: Given here is a list of the basic divisions of the book (sometimes page by page, in complex cases) and an indication of the important ornithological material contained. (5) Discussion: This section is usually brief, clarifying the history of the publication, noting interesting peculiarities, and often citing further discussion elsewhere. An attempt is made to place the importance of the work in historical and ornithological perspective. (6) References: Supplementary bibliographic references as well as citations to reviews are listed.

The bibliographic detail included in this catalogue far surpasses earlier efforts. This is in part due to the greater quantity of material at hand and to the opportunity to build on past scholarship. But it is also a result of the erudition and herculean efforts of Robert Mengel.

We can only hope that the remaining volumes of the catalogue (only partially compiled by Mengel) will be "published without undue delay" as promised by the University of Kansas Libraries.

These volumes are essential reference materials for anyone with an interest in bibliography or in the history of ornithology; indeed, anyone using the literature covered in its pages would be aided by this work.—D. Scott Wood.

Sexual Selection, Lek and Arena Behavior, and Sexual Size Dimorphism in Birds. By Robert B. Payne. Ornithological Monographs No. 33, American Ornithologists' Union, Washington, D.C., 1984:52 pp., 12 figs. $8.00 ($6.50, members).—Reading this monograph is a must for all students of sexual selection and avian size dimorphism, for its author has compiled and summarized an enormous amount of relevant information.

The monograph consists of three major parts: (1) "Intensity of sexual selection": prizes for the winners in different mating systems, (2) "Male competition and female choice of mates": modes of sexual selection and alternative mating strategies, and (3) "Sexual dimorphism and sexual selection." The final section comprises two-thirds of the monograph; the middle section is only three pages in length. The greatest strength of the monograph lies in section one, where the author moves through a useful and logical discussion of various ways to measure variance in reproductive success. This is followed by his adoption of an index in sexual selection intensity adopted from theoretical population genetics: $I_{m(f)}$ = the ratio of variance in the number of mates per male (female) to the square of the mean number of mates. He also uses the evenness statistic *J*.

These measures, and the variance itself, are applied to the following questions: (1) are males in lekking and other arena species subject to more intense sexual selection than are males in monogamous species, and (2) are males in lekking and polygynous species under more intense selection than are females? The data presented indicate that the answers are yes. Payne brings up many interesting subjects for future discussion, e.g., how does the intensity of sexual selection vary among years and populations, and what environmental and social factors bring about this variation? A much better data base for polygynous species is needed before anything definitive can be said relative to the intensity of sexual selection to which birds with this type of mating system are exposed, and data might have been presented for a greater variety of monogamous species (e.g., waterfowl).

Payne's lumping of all species with promiscuous mating systems is questionable. He, himself, points out that these species vary on a continuum with regard to the degree of clumping. They may well vary enormously in the intensity of sexual selection, and this question should be tested rigorously. In Table 4, which summarizes the intensity of sexual selection among females, there are four errors in the use of +/− signs comparing male and female variation in sexual selection pressure.

The second section is directed at answering the questions: (1) do males in the lekking and arena species compete among themselves by direct fighting, including both physical combat and aggressive displays, rather than by alternative mating strategies, and (2) does male competition explain the success of males in attracting females? The three pages allocated to this part of the paper are inadequate. In fact, the data available for addressing these questions are so weak that it is questionable whether this discussion should have been included in the monograph.

The third section is directed at the question: are the evolutionary results of sexual selection in sexual size dimorphism more pronounced in lekking birds than in their nonlekking relatives? In this section, 12 figures plot male/female size against female wing length; size dimorphism relative to mating system is presented in detailed tabular form for manakins. This compilation of information is extremely useful, and will serve as a ready reference for

years to come. In some cases, the usefulness of the figures might be enhanced by labeling of the species or genera concerned. The author should have been more careful in assigning species to various mating systems, e.g., on p. 20, he says "Polygynous mating systems are known for Temminck's Stint (*Calidris temminckii*), Little Stint (*C. minute*), Sanderling (*C. alba*), White-rumped Sandpiper (*C. fuscicollis*), Curlew Sandpiper (*C. ferruginea*) and Sharp-tailed Sandpiper (*C. acuminata*)." However, upon careful examination of the literature, one finds that two species, Curlew and Sharp-tailed Sandpipers, are probably polygynous but data are inadequate to allow a definitive statement to that effect. Of the three remaining species, none is polygynous. Temminck's Stints are truly *polygamous* (i.e., both sexes are polygamous in a single season); and this also is probably the case in Little Stint. The situation for Sanderlings is not clear: in one population monogamy prevailed, and in another there were indications that both males and females breed with two mates in a year, but data are inconclusive. It might also be noted here that these are calidridine sandpipers, not "calidrine."

In summary, Payne has done a great service in presenting a large variety of information on the intensity of sexual selection and its consequences on size in birds. Again, all students of sexual selection in birds and of avian social systems in general should read this monograph.—Lewis W. Oring.

Life History Studies of Woodpeckers of Eastern North America. By Lawrence Kilham, illus. by Jane Kilham. Nuttall Ornithological Club, Publication No. 20, 1983:240 pp., Frontispiece, 58 numbered text figs. $19.00.—Larry Kilham has been recognized for several decades as an author of numerous articles on woodpecker biology and behavior. This recent book is a summarization, revision, and expansion of 51 articles and notes published in a variety of ornithological journals over the past 25 years. The book is a wealth of descriptive narration on the behavior of most eastern North American woodpeckers. The behaviors of Downy (*Picoides pubescens*), Hairy (*P. villosus*), Pileated (*Dryocopus pileatus*), Red-bellied (*Melanerpes carolinus*), and Red-headed (*M. erythrocephalus*) woodpeckers , as well as Yellow-bellied Sapsuckers (*Sphyrapicus varius*) and Northern Flickers (*Colaptes auratus*), are presented in greatest detail. Aspects of foraging behavior, behavior early in the breeding season, nesting, postnesting, and methods of communication are described and discussed to various degrees for each of the 7 species. Excellent narrations of selected behavioral patterns and intra- and interspecific interactions provide valuable behavioral information in an entertaining fashion. A short chapter in the book presents selected nesting behavior of Black-backed Woodpeckers (*Picoides arcticus*) and methods of communication. A chapter dealing with behavior of two Central American species of woodpeckers, the Crimson-crested (*Campephilus melanoleucos*) and Pale-billed (*C. guatemalensis*) woodpeckers, seemed slightly out of place in the book. The author includes this chapter, however, to provide behavioral descriptions of species similar to the Ivory-billed Woodpecker (*C. principalis*). No information is presented on the two other eastern North American woodpeckers, the Three-toed (*Picoides tridactylus*) and Red-cockaded (*P. borealis*) woodpeckers. Two final chapters in the book discuss selected aspects of behavior and morphology, and make general conclusions about woodpecker behavior.

Although overall organization in the book is good, one section on Pileated Woodpecker vocalizations (p. 90) probably should have been included under the general heading of vocalizations on p. 110. Also, the section on how Red-crowned Woodpeckers (*Melanerpes rubricapillus*) enter their nest holes seems a bit out of place in the chapter on the Red-bellied Woodpecker. The book does not approach woodpecker behavior from a quantitative point of view; however, sample sizes for many observations are presented. Not all recent literature is included in the book, but as the author states in the preface, his objective was to focus

mainly on his own observations rather than include everything known about the woodpeckers of eastern North America.

The book is an engaging narration rather than a formal scientific presentation. Much of Larry Kilham's humor and amiable disposition can be gleaned from the lines. The style is animated, and enables the reader to form easily a mental picture of the behavior, displays, and interactions of woodpeckers. As an amateur ornithologist, Larry Kilham has made more of a contribution to science and woodpecker biology than many professionals. This book provides an excellent, readable consolidation of his 25 years of observations in one monograph. I recommend the book to both amateur and professional ornithologists who are interested specifically in woodpeckers or avian behavior in general.—Richard N. Conner.

Kirtland's Warbler: The Natural History of an Endangered Species. By Lawrence H. Walkinshaw. Bulletin 58, Cranbrook Institute of Science, Bloomfield Hills, Michigan, 1983:207 pp., 45 numbered text figs., 55 tables. $11.95.—Lawrence H. Walkinshaw's acquaintance with the Kirtland's Warbler (*Dendroica kirtlandii*) spans more than a half-century, beginning in 1931 when he found his first nest on the species' restricted breeding range in the north-central portion of Michigan's Lower Peninsula. Dr. Walkinshaw has drawn on this considerable personal experience and combined it with the published literature and data that he collected during the 1966–1977 breeding seasons to produce a book that details many features of the Kirtland's Warbler's breeding biology. Each chapter is devoted to one of the topics typically covered in life-history studies, and one chapter, written by Mark Bergland, presents a statistical analysis of the factors influencing nesting success.

The style of the book is that of straightforward presentation of data. Considerable attention is given to vegetation characteristics of territories and nest sites, within- and between-year movements of adults and returning young, and reproductive histories of banded birds. Descriptive statistics are employed, but statistical comparisons are rarely made.

Most of the data were collected after the publication of Harold Mayfield's book (The Kirtland's Warbler, Cranbrook Institute of Science, Bloomfield Hills, Michigan, 1960), so the results of the two studies are a store of valuable information on this endangered species. Because Dr. Walkinshaw's studies were conducted immediately before and during the time that thousands of Brown-headed Cowbirds (*Molothrus ater*) were removed from the warbler's breeding grounds, they record the warbler's response to this large-scale experiment. Cowbird removal has led to decreased parasitism and to increased reproductive success of Kirtland's Warbler, but not to an increased breeding population.

The central feature of this book is its presentation of detailed information about individual birds, information that others can analyze for their own purposes. The usefulness of these data are occasionally marred by inconsistencies. Table 1 (p. 7) lists four males banded as nestlings in 1974 as returning in subsequent years, but Table 13 (p. 44) lists five as returning to Michigan plus one as being recaptured in Quebec. Similarly, Table 1 has 16 females banded as nestlings returning as breeding birds, whereas Table 14 (p. 48) lists 20 as returning. Such discrepancies, as well as repetitive statements and unexpected placement of topics (e.g., a section on mortality of adults in the chapter on nesting success), suggest that chapters were sometimes written without due consideration for the organization of the whole. But the value of the data contained in this book outweighs such shortcomings. The ornithological community owes thanks to Dr. Walkinshaw for collecting, compiling, and making available these hard-to-obtain data on this rare species.—Charles F. Thompson.

Population Ecology of the Bobwhite. By John L. Roseberry and William D. Klimstra. Southern Illinois Univ. Press, Carbondale, Illinois, 1984:282 pp., 23 photographic illustrations, 45 text figures, 26 tables. $25.00.—The Northern Bobwhite (*Colinus virginianus*), one

of my favorite birds, is becoming increasingly rare in the northern and central United States, a victim of habitat deterioration and destruction. The bird has been the subject of intensive studies, and has been described in numerous state conservation department publications and innumerable papers, including monographs on southern populations by Herbert Stoddard (The Bobwhite Quail: its Habits, Preservation, and Increase, Charles Scribner's Sons, New York, New York, 1931) and W. Rosene (The Bobwhite Quail: its Life and Management, Rutgers Univ. Press, New Brunswick, New Jersey, 1969), and on northern populations at the periphery of the species' range by C. Kabat and D. R. Thompson (Wisconsin Quail, 1834–1962—Population Dynamics and Habitat Management, Wisconsin Conserv. Dept. Tech. Bull. 30, 1963) and by P. Errington (Ecol. Monogr. 15: 1–34, 1945). Thus I looked forward to this book on the bobwhite in the central part of its range, which would fill the gap between the studies of northern and southern birds.

The objective of this 27-year study was to investigate the ecology and population dynamics of a hunted but unmanaged bobwhite population in a changing agricultural environment. The study area was 627 ha of privately owned farmland 7 km northeast of Carbondale, Illinois, near the center of the species' geographic range.

Because the study produced a number of important papers on the bobwhite, I thought the book would be a definitive study on midwestern bobwhite. Instead, the book is not only on quail ecology but also on "broader questions relating to population regulation." The ecology and population dynamics of the bobwhite in southern Illinois are lost in its pages. Why did the authors choose such an approach? One of the reasons emerges between the lines of the Preface. The authors seem to apologize for spending so much time "plowing old ground" and go to some lengths to defend their study. So instead of presenting and integrating all of their findings, including those previously published, they opted for a more general book.

The book starts out well. Chapter 1 explains the background and approach of the study. Chapter 2 describes the study area. And Chapter 3 on habitat needs and utilization, augmented by 19 pages of photographs, tells the story of habitat changes and decline. But from this point on, the book begins to fall apart. The next four chapters discuss, in order, fall and winter losses, recruitment, abundance, and exploitation. The data, backed by graphs and tables, are there, but they are scattered within tedious discussions of the literature on both bobwhite and general population ecology. The only way one can follow the story of the bobwhite in southern Illinois is to make notes as one reads. The reader has to become much like a bobwhite, scratching among litter and chaff seeking grains of corn. The authors at least could have provided the reader with chapter summaries of their data, which would have improved the book immensely.

The book contains a lot of excellent data, valuable for students of population ecology. For example, one learns that the population density in southern Illinois is 62 birds per 100 ha, exceptionally high for an unmanaged population; and that annual rates of summer gain were strongly influenced by (1) the number of days of winter snow cover (especially in late winter) $\geq$2.5 cm; (2) the ratio of breeding density by *K*; (3) the number of crop fields $\geq$4.5 ha present the previous autumn; and (4) the total rainfall in early spring. Over 27 years the population experienced fluctuations approximately every 3.5 years, fitting Palmgren's and Cole's (J. Wildl. Manage. 15:233–252, 1951) prediction for serially correlated but random oscillations in populations. There were two major peaks about 9 years apart, but the peaks were not that prominent compared to those of cyclic boreal species.

Chapter 8, which takes up 22% of the basic text, deals with population regulation. In this chapter the authors attempt to show that the quail in this study experienced density-dependent population regulation and cyclic fluctuations. They attribute population regulation to a rather ambiguous population momentum—the tendency of a population to overshoot

K on the upswing—and the damping effects of compensatory reproduction and mortality. They attempt to demonstrate that bobwhites in southern Illinois follow a 10-year cycle. (For some reason wildlife biologists have an unrequited love affair with cycles.) As a treatment of population regulation, Chapter 8 is badly flawed. The authors rely on theories and literature of the 1940s, 1950s, and 1960s, now largely historical. They obviously are unfamiliar with experimental and theoretical population ecology of the late 1970s and 1980s, which they could have used to advantage with their volume of data. Instead, they flirt with group selection and embrace extrinsic rather than intrinsic influences on population regulation. They spend well over half the chapter advancing their argument that quail populations in southern Illinois follow a 10-year cycle. They demonstrate that the two major peaks of roughly nine years fit the nodal lunar cycle index proposed by Archibald (Wildl. Soc. Bull. 5:126–129, 1977) to explain the 10-year cycles in boreal animals. Archibald based this index on the astronomical fact that the moon does not follow the path of the sun. It has a nodal cycle of 18.6 years and cuts across the elliptical arc of the sun once every 9.3 years. This nodal cycle causes apparent changes in the declination of the moon and an annual time lag in moonrise and moonset. The lag in moonrise, which is most pronounced around the vernal equinox, means that at regular intervals moonrise comes some time after sunset rather than at sunset, subjecting organisms to strong illumination by the moon after a period of darkness. The authors hint that perhaps this cyclic exposure to light in the bird's circadian rhythm would influence reproduction. With all the data at hand, the authors could have spent their time much more profitably investigating intrinsic mechanisms based on modern population theory which desperately needs to be tested on the kind of data they have accumulated.

Now that the authors have expressed their ideas on population regulation, they ought to write the book they should have written, a monograph on the long-term population study of Northern Bobwhite in the agricultural midwest and not worry about plowing old ground.—Robert Leo Smith.

The Seaside Sparrow, its Biology and Management. By Thomas L. Quay, John B. Funderburg Jr., David S. Lee, Eloise F. Potter, and Chandler S. Robbins (eds.). Occasional Papers of the North Carolina Biological Survey, Raleigh, North Carolina. 1983:174 pp., one colored plate, many maps and text figs., one 7-inch plastic record. $15.00.—In October 1981 a symposium on the Seaside Sparrow (*Ammodramus maritimus*) was held at the North Carolina State Museum, and somewhat belatedly we have an interesting volume containing the proceedings of that meeting. On opening the book we are immediately confronted with an attractive color plate by John Henry Dick illustrating the nine races of the species, including those forms *mirabilis* and *nigrescens* formerly considered as distinct species. What follows is equally interesting.

Part I of the symposium, "The Seaside Sparrow: An Overview," contains a keynote speech by E. J. Hester, a discussion of The Salt-marsh Ecosystem by A. W. Cooper, a general discussion of the Seaside Sparrow assemblage by O. L. Austin Jr., and a very stimulating paper by J. B. Funderburg and T. L. Quay on The Distributional Evolution of the Seaside Sparrow. Part II, "The Biology of the Seaside Sparrow," contains 10 papers on a variety of topics. Of these, the detailed discussion of the Cape Sable Sparrow (*mirabilis*) by H. W. Werner and G. E. Woolfenden presents the most original information. Two papers by J. W. Hardy and M. V. McDonald on vocalizations are illustrated with a small plastic "floppy" record that is inserted in the book. The other papers in this section present some specific biological information. Part III, "Protection and Management of Seaside Sparrow Populations," discusses the habitat use of the Cape Sable Sparrow (by J. A. Kushlan and O. L. Bass Jr.), the use of fire in the management on the Cape Sable Sparrow (by D. L. Taylor),

the possiblity of breeding Seaside Sparrows in captivity, and a summary paper by E. F. Potter.

The Seaside Sparrow, with its extensive but exceedingly narrow breeding range in the coastal salt marshes, is a fascinating species. All the authors emphasize that the salt marsh habitat is at peril throughout, and so all forms of *A. maritimus* are in some danger. As is well known, *nigrescens* is extinct in the wild and, at present, only a handful of (possibly senescent) males remain in captivity. The time lag in publishing this symposium results in giving a somewhat optimistic view of the possibility of preserving the Dusky Seaside by cross-breeding that conflicts with the rather gloomy results obtained so far. The race *pelonota* is extinct and both of these forms have been eliminated by habitat destruction and changes. On the other hand, the race *mirabilis* seems to be doing as well as can be expected, and Kushlan and Bass give an estimate of a population of 6000 in 1981.

There is some repetition in the symposium, as at least three authors recount the checkered history of *mirabilis,* but the level of the papers is above the general run of symposium volumes. The collection is well worth reading.—George A. Hall.

Behavior of Fledgling Peregrines. By Steve K. Sherrod. The Peregrine Fund, Ithaca, New York, 1983:213 pp., 59 figures. $17.00 paper.—This is a detailed study of the behavior of young *Falco peregrinus* from the last week of the nestling period through the time the birds depart the vicinity of the nest. Two broods in Greenland and two in Australia were watched for a total of 1040 h, and three hand-reared broods placed in the wild were watched for 1350 h in the U.S. All young were fitted with radio transmitters, which facilitated tracking of the birds once they began to range widely. The hand-reared birds were produced in the facilities of the Peregrine Fund and transported to the release site at an age of four weeks and allowed liberty at an age of six weeks. Food was provided at the artificial nest site through the twelfth week.

The book contains much valuable information and a few new interpretations of the development of behavior in young peregrines. The results are usually presented in tables or graphs, supplemented with drawings and selected excerpts from field notes. The drawings, by K. L. Allaben-Confer, are very attractive and informative. The graphs appear to be produced by a microcomputer with a program of low resolution; they are not only crude, but often are difficult to decipher and comprehend. Conclusions are generally well-supported by data or at least by several anecodotal accounts, but there are at least a few notable exceptions in which the documentation appears to be not much more than the author's opinion. Falconry terminology is used liberally, usually without explanation, and a few readers may not be able to "hack-it" and may "throw-up." (Hacking is a falconer's method of allowing young falcons, taken from the nest, to fly free after they fledge, returning to the hack-site to be fed by the falconer. Throwing-up is a sudden, upward swoop of a falcon in flight.) An example of the confusion that can result from the use of this terminology: (speaking of a trained falcon) ". . . it is allowed to eat as much as it wishes from the animal after the kill, even though the falcon will be too fat to fly for a day or two afterwards" (pp. 91–92). A single meal does not render a falcon flightless for a day or two; the bird simply has too much stored fat to be flown safely by the falconer. The bond between falcon and falconer is simply hunger: a bird that is not starved will not return to the falconer and will be lost to the wild.

I noticed only four typographical errors; three are extremely minor, but the fourth is a bit confusing: Parts A and B of Fig. 26 appear to be transposed, and since they happen to be printed on opposite sides of a page the mistake is not immediately obvious. Entomologists will be surprised that grasshoppers and crickets are in the order Odonata (p. 50). With these exceptions, the book is reasonably well organized and written with sufficient clarity.

Chapter 3, "Leaving the nest," illustrates both the strengths and weaknesses of this work, although probably more of the latter. Most of the chapter is devoted to age and other factors determining first flight. The variation in age at fledging (39–49 days post-hatch) is well documented in Table 1. The author indicates that the youngest bird in a brood usually is the last to fledge but the oldest is not always the first to fly. This is supported by the data in Table 4, but relative age (within a brood and sex) was determined by the length of the longest rectrix when the young were about four weeks old. Furthermore, observations at nests were made only every fourth day, raising some question as to whether or not the "first sustained flight" of a young was observed. The influence of brood size on age of fledging is supported only by the citation of an unpublished dissertation. The author believes that hunger can influence fledging but offers no direct evidence. The behavior of siblings is also said to influence fledging; this is supported by an observation of one young flying 10 m, escaping its siblings who were after the food it had just obtained from its parents. The author can "state with certainty" that larger geographic variants of the peregrine develop more slowly than smaller ones, although he admits he has no growth data. "Thus, . . . the larger geographic variants . . . do in fact first fly at a slightly older age." An examination of Table 1 reveals not even a suggestion of support for this statement. Perhaps larger races of peregrines do develop more slowly than smaller ones; this possibility of intraspecific variation is worth documentation. The last third of the chapter is an excellent and thorough presentation of data and arguments that I believe effectively disproves the hypothesis that adult peregrines lure their young into their first flight. This is a popular hypothesis for not only peregrines and other raptors but for many other kinds of birds as well. Sherrod's hypothesis is probably valid for all of these species: adults fly about in front of the nest with prey not to lure their young into flight but because they are reluctant to land among their large and aggressively hungry young. He describes several very aggressive "attacks" by young on their parents. In one case, a male delivering prey was footed in the wing by one of his offspring and grasped on the head by the beak of another; the young pulling in opposite directions on the complaining adult for seven seconds before he managed to give the food to one of them, resulting in both young releasing their parent.

I disagree with several of Sherrod's interpretations of his observations. He speculates that peregrine family units remain intact through at least part of migration. His evidence for this is very questionable. He notes that "sometimes" young peregrines sit "together or at least very closely on beaches of the Texas coast." "Often" these birds exhibited "similar color morphs." Sherrod and two other Texas trappers "think it possible that these groups are composed of siblings." The next bit of evidence comes from a falconer trapping birds on beaches on the east coast who observed that young birds begging in the vicinity of adults "was so commonplace [that] he made no particular note of it." In my considerable experience, the impressions and conclusions of falconers and other aviculturists are only rarely reliable scientific information. I should also note that no evidence is presented to suggest that an adult actually fed young. Sherrod's key evidence is from six days of incidental watching of over 30 "groups" of migrating American Kestrels (*Falco sparverius*) in Maryland. I quote: "the groups were comprised of one to five individuals. When I saw two young begging vocally and flying in a flutter-glide behind an adult female, I finally realized that at least some of the larger parties were in fact family groups. Later, I watched as an adult flying in front of another begging youngster, grabbed an insect out of the air and transferred it to her offspring." It is sufficiently difficult to determine the age of *F. sparverius* in the hand that I would be hesitant to guess the age of any kestrel observed in flight, even at short range and with the best optical aids available. Sherrod, however, has not only determined the age of the birds but has identified some as the offspring of a particular female. In more than 30 years of watching migrating hawks and falcons, I have never observed an incident that I

would begin to interpret as adults feeding young. I have observed many incidents of attempted piracy, piracy, and other interactions that, when identifiable, usually were between birds of the same age class. I hope that this is the only case where Sherrod's "facts" were the result of his preconceptions.

Sherrod describes a number of incidents in which satiated young aggressively drove off adults that were attempting to glean uneaten food items for themselves. Most of the attacks occurred well before the young were able to provide for themselves, and several appeared to be of sufficient violence to endanger the parent. In one incident, both parents made about 20 attempts over a 3-h period to retrieve a pigeon that their three satiated young were not eating. The parents were footed by the young six times, of which two cases involved a young grasping her mother's breast with both feet and remaining impaled until both birds fell off the ledge in the struggle. Sherrod interprets these observations as a "perfect example" of parent-offspring conflict (Trivers, Am. Zool. 14:249–264, 1974). Inflicting damage on one's parent which may impair or eliminate the parent's ability to provide one with sustenance that one cannot obtain alone is not selfish, it is pathological, and certainly does not increase one's inclusive fitness. The persistance of the parents in attempting to retrieve the pigeon suggests that this was a valuable resource to them, and I find Sherrod's explanation of the selfish, aggressive behavior of the young in depriving their parents of this food wanting.

Sherrod notes that the coefficient of relationship, *r*, between young and their parents is only 0.5 while *r* to themselves is 1. He fails to realize that *r* also is 0.5 between the young peregrine and the offspring it might produce in the future, which is exactly equal to the *r* between the young peregrine and siblings which might be produced by its parents in the future. Peregrines rarely breed until they are two years old and mortality of individuals is higher for birds in their first year than in subsequent years. The probability of a young peregrine's parents surviving to produce siblings of the young is thus greater than the young surviving to produce its own offspring. For example, Enderson (*In* J. J. Hickey, ed. Peregrine Falcon Populations. Univ. Wisconsin Press Madison, Wisconsin, 1969) gives the mortality of peregrines as 70% in the first year of life and 25% for subsequent years. The probability of a young peregrine surviving two years to reproduce is, thus, $0.30 \times 0.75 = 0.23$. In contrast, the probability of both of a young peregrine's parents surviving and reproducing during those two years is $0.75^2 + 0.75^4 = 0.88$. Thus, a young peregrine's parents have 3.9 times the potential to produce siblings of the young than it has to produce its own offspring during its first two years of life. This leads to the prediction that young peregrines should avoid conflict with their parents and demand no more than they need for their own survival.

Why, then, did Sherrod's young peregrines behave so aggressively to their parents? Almost all of the aggresive incidents occurred at the Australian nests, where food deliveries were relatively infrequent and consisted of larger prey than in Greenland. I suggest that infrequent deliveries of large prey produced the excessively aggressive behavior of the young to their parents: a full crop may not suffice to eliminate the "hunger drive" of a young animal subjected to frequent food deprivation. I am aware that this explanation deals only with proximate causes but it offers a reason for why an explanation based on ultimate, or evolutionary, causes fails to explain the behaviors. Parent-offspring conflict is a plausible explanation for some behavior in raptors (Mueller et al., Wilson Bull. 93:85–92, 1981), but it cannot be used where the possible benefits to young are smaller than the costs to the adults.

I find serious fault with essentially all of Sherrod's analyses of the development of behavior in young peregrines because he appears to be unaware of the concept of maturation. He allows that "young Peregrines do innately recognize flying prey as the potential target." But he then goes on: "The hundreds of pursuits which the young falcons make after prey furnish the trial-and-error learning necessary to recognize and capture the individual species. The

association which finally occurs between capture and feeding completes the predatory sequence" (p. 117). Sherrod notes that very young falcons are afraid of potential prey and suggests that they must become habituated to prey before they can kill and that reinforcement is necessary for a falcon to develop an association between "pursued prey and food" (p. 91). Sherrod's review of the literature on the development of predatory behavior is reasonably extensive, and it is thus surprising that he is apparently unaware of the one experimental study performed on *Falco*. I have shown (Mueller, Behaviour 49:313–324, 1974) that hand-reared, naive American Kestrels, at an age of 10 weeks or older, will recognize mice as prey and attack and kill mice in a manner indistinguishable from adults without prior experience, habituation, practice, or reinforcement. Sherman (Auk 30:406–418, 1913) has shown that nestling American Kestrels show either fear or no response to live prey. It is apparent that the essentials of prey recognition, capture, and killing are innate in *F. sparverius* but appear in a bird's behavioral repertoire only when it has matured to an age where those behaviors are appropriate. There is nothing in Sherrod's observations that is inconsistent with a similar development of predatory behavior in *F. peregrinus*.

I have severely criticized several of Sherrod's interpretations of his observations. I feel, however, his book is an invaluable contribution and belongs on the bookshelf of all biologists interested in raptors or in the development of behavior in birds.—Helmut C. Mueller

Nature Through Tropical Windows. By Alexander F. Skutch, illus. by Dana Gardner. University of California Press, Berkeley, California, 1983:374 pp. $19.95.—The ability to write gripping factual accounts of the everyday activities of animals and plants is one that few of us possess. Skutch's numerous treatises on tropical natural history are always beautifully and flawlessly crafted, and the present volume is no exception. Strictly speaking, however, they are not entirely factual. This is not to suggest that they contain misinformation, but rather that they present facts that are frequently interpreted through the heart rather than through the objective mind. But it is difficult to be objective all day long, and Skutch's gentle musings on Nature's mysteries provide a (usually) fairly palatable matrix through which the weary mind may rapidly soak up a tremendous amount of material.

Having said that, I suppose I have no right to claim that the weary mind requires the scientific names of all organisms in order to grasp the gist of the story, but I did find that this omission somewhat impeded my ability to file information. The chapters on botany are better in this regard. They are also less sentimental. I was especially struck with the following statement from a chapter called "A favorite food of birds": "Apparently, the kind of fruit that a plant produces depends largely upon its evolutionary history and the vagaries of mutation. Possibly, too, it is related to the chemistry of the edible tissues." This casual tribute to stochasticity is almost startling in the midst of the portrait of determinism that emerges from Skutch's book.

The book's 18 chapters include 8 that are expressly about birds, 4 on botany and the relationships of plants and animals, 2 on general natural history placed in an evolutionary milieu, and 4 rather personal treatises that might go under the heading of "religion without revelation." The modesty of the Bibliography reflects two things: first, that much of the information being presented is new; second, that the information is not always completely integrated with what is not new. For example, the interesting account of *Piper* biology ends with speculation about the possible pollinators of these plants. Much work has already been done on the pollination ecology of Costa Rican *Piper,* however, and it is known that bats play the dominant role in it (e.g., Fleming, T. H., et al., Ecology 58:619–627, 1977; Heithaus, E. R. and T. H. Fleming, Ecol. Monogr. 48:127–143, 1978). Neither of these works is mentioned. I was disturbed, too, by Skutch's attitude towards current evolutionary theory in the chapter entitled "Selfishness, altruism, and cooperation." He is uncomfortable with

the implications of the "selfish gene" doctrine and the possibility that there is no particular reason for the existence of life on Earth: ". . . evolution can occur only in populations, never in individuals, and unless the competing individuals also cooperate to perpetuate the species, it will vanish from the Earth." This is one baby that should have followed the bathwater.

My reactions to this book are, obviously, mixed. To label it as a book for nature lovers would be to dismiss it with unfair superficiality. To leave it for the intelligent layman would be to deny biologists access to a treasure trove of first-hand information available nowhere else. But it delves too deeply, for my taste, into realms far beyond that of the natural world. If you are a biologist seeking unadorned facts on tropical natural history, I highly recommend that you read this book. Do it selectively, however, and with a salt shaker by your side.—MARY C. MCKITRICK.

FIRST VICE-PRESIDENTS OF THE WILSON ORNITHOLOGICAL SOCIETY

In anticipation of the 100th anniversary of The Wilson Ornithological Society, The Wilson Bulletin is publishing a series of lists compiled by John L. Zimmerman of the past and present officers and Council Members of the Society. Below is a list of the First Vice-Presidents of The Wilson Ornithological Society.

C. C. Maxfield, 1893
R. M. Strong, 1894
Ned Hollister, 1895–1903
W. L. Dawson, 1904–1905
R. L. Baird, 1906–1908
W. E. Saunders, 1909–1911
B. H. Swales, 1912–1913
Geo. L. Fordyce, 1914–1919
Harry C. Oberholser, 1920–1921
Dayton Stoner, 1922–1923
Wm. I. Lyon, 1924
Thos. H. Whitney, 1925–1928
George Miksch Sutton, 1929–1931
Edwin L. Mosely, 1932
Josselyn Van Tyne, 1933–1934
Alfred M. Bailey, 1935–1936
Margaret Morse Nice, 1937
Lawrence E. Hicks, 1938–1939
George Miksch Sutton, 1940–1941
S. Charles Kendeigh, 1942–1943
Olin Sewall Pettingill, Jr., 1944–1947
Maurice Brooks, 1948–1950
Walter J. Breckenridge, 1950–1952
Burt L. Monroe, Sr., 1952–1954
Harold F. Mayfield, 1954–1955
John T. Emlen, Jr., 1955–1956
Lawrence H. Walkinshaw, 1956–1958
Harold F. Mayfield, 1958–1960
Phillips B. Street, 1960–1962
Roger Tory Peterson, 1962–1964
Aaron M. Bagg, 1964–1966
H. Lewis Batts, Jr., 1966–1968
William W. H. Gunn, 1968–1969
Pershing B. Hofslund, 1969–1971
Kenneth C. Parkes, 1971–1973
Andrew J. Berger, 1973–1975
Douglas A. James, 1975–1977
George A. Hall, 1977–1979
Abbot S. Gaunt, 1979–1981
Jerome A. Jackson, 1981–1983
Clait E. Braun, 1983–

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SPECIAL CONSERVATION REVIEW

GUAM: A PROBLEM IN AVIAN CONSERVATION

THE NATIVE FOREST BIRDS OF GUAM. Ornithological Monographs No. 31. By J. Mark Jenkins. American Ornithologists' Union, Washington D.C., 1983:61 pp., color frontispiece, 6 color plates with caption figs., 14 range maps included among 24 numbered text figs., 6 tables. $9.00 ($7.00 to AOU members). NATURAL HISTORY OF THE GUAM RAIL. By J. Mark Jenkins. Condor 81:404–408, 1979. FOREST BIRDS OF GUAM. By John Engbring. Endangered Species Technical Bulletin 8:6–7, 1983 (January). GUAM: PARADISE LOST FOR WILDLIFE. By Julie A. Savidge. Biological Conservation 30:305–317, 1984.—I compliment the Division of Aquatic and Wildlife Resources, Department of Agriculture, Government of Guam, for sponsoring the biological field studies on Guam by Mark Jenkins, their staff, and visiting scientists from other agencies. These resulting papers, based on data gathered by the Division going back to 1960, are a response to the crisis occasioned by the sudden collapse of forest bird populations during the 1970s. In August 1978 the Division proposed seven bird species and two fruit bats (*Pteropus mariannus* and *P. tokudae*) of Guam for inclusion on the U.S. Endangered Species List. Actual listing did not transpire until 27 Aug. 1984.

The monograph by Mark Jenkins consists principally of 11 species accounts. Each starts with the name of the bird, followed by paragraphs under headings of description, distribution, habitat, behavior, food habits, nesting, and status on Guam. A graph for each species shows changes in numbers from 1974 to 1979 based on standardized road counts and station counts, whereas shading on a map indicates distribution and abundance on Guam in 1979. Photographs of eight forest species are displayed, most of them in color. Two color views of "limestone forest" show the area where nearly all native Guam bird species were concentrated during 1978 and 1979. Conclusions are that by 1979 the native forest birds of Guam occupied only 5–10% of their historical island-wide distributions; that they had contracted into the northern tip of the island; that abundant suitable habitat was now vacant; and that most of these bird species were in immediate danger of extinction.

The monograph is designed for professional zoologists. Nevertheless the color photos of gorgeous Micronesian birds, the ample size of graphs and maps, and a direct writing style make the grim message perfectly understandable to conservationists and amateurs. Absence of encumbering technical terms and mumbo-jumbo from ecology and "island biogeography" is gratifying. What good are equilibrium formulae in a crisis like this?

The author's aim is to bring together what is known of Guamanian birds, to compare their historical distribution and abundance with that of the present, to encourage further study, and to "stimulate concern for a unique and disappearing avifauna." In this he succeeds. Reading the book is a good start for learning about the Micronesian avifauna and for understanding how to avoid similar catastrophes on other islands. Editing and printing is up to the high standards of the AOU Monograph series. I object only to the habitat photographs that do not look like forest—the majestic rain forest that Rollin Baker, David Johnson, Henry Dybas, and I walked beneath at Ritidian Point in 1945. I thought "No wonder the birds are going, if they have only these bushes and weeds to live in." I am assured by recent visitors to Guam, however, that these scenes portray some of the original canopy of trees, of stature commensurate with the tall palms seen along the beach in the lower plate (p. 27).

Although there was no delay in publication once the manuscript was received, the fact is that Mark Jenkins' monograph and his companion piece on the Guam Rail (*Rallus owstoni*) bring us only up to 1979! After that, things begin to happen fast. Jenkins' dire predictions

are largely fulfilled. The Division of Aquatic and Wildlife Resources had to make another survey with John Engbring in 1981 and had to grapple with the disease-versus-predation problem soon thereafter, with the help of Julie Savidge. Engbring's results and a preview of the course of Ms. Savidge's research, together with a good bibliography on the entire biota, are in the two additional papers listed at the head of this review.

Minor errors or sources of misunderstandings include Jenkins' belief that introduction of the giant African snail (*Achetina fulica*) influenced the Guam Rail to become an eater of gastropods. Actually a rich native fauna of snails and slugs had nourished the rail as it did the Nightingale Reed-warbler (*Acrocephalus luscinia*). Was this natural food source destroyed by the predatory snail and flatworm introduced for biological control of *Achetina*? Jenkins uses a misnomer for the brown tree snake, *Boiga irregularis*. He calls it the "Philippine rat snake," a name that applies to *Elaphe erythrura*. *Boiga irregularis* does not occur in the Philippines, was first found on Guam in 1947, was probably carried in by the military from New Guinea or Biak during World War II, finds its most apt common name in the German "Nacht Baumnatter" or nocturnal tree-adder, and is well known as a predator of birds and their eggs in Australia. Ms. Savidge refers to Rota, Tinian, and Saipan as "the Northern Marianas," a recently formed political unit. But in the biological literature, "northern Marianas" refers to smaller, volcanic islands farther north. There, in 1979, Roger Clapp of the Biological Survey Section, U.S. Fish and Wildlife Service, found large sea bird colonies. He reported that hunters were taking Marianas fruit bats (*Pteropus mariannus*) for the Guam market, and that abundant Micronesian Megapodes (*Megapodius laperouse*) deposited their eggs in gravel warmed by the volcanos.

Because Jenkins' population estimates unfortunately no longer reflect present numbers, I should depart from the ordinary review at this point and bring the story up to the beginning of 1985, in the form of an annotated species list. It is based in part on Julie Savidge's presentation at the 1983 New York meeting of the AOU. I have developed the remaining story—I hope I have it all straight—from correspondence or conversations with biologists who have studied or are now studying the flora and fauna of Guam. At the 1983 centennial meeting of the AOU, Ms. Julie Savidge, whose work is another credit to the Division of Aquatic and Wildlife Resources, took by surprise a standing-room-only audience who came to hear her presentation of "Reasons for the decline of Guam's avifauna." Ms. Savidge presented circumstantial evidence incriminating *Boiga irregularis*. For each of a series of time-lapses, the distribution maps of the snake's northward expansion complemented those of the retreating bird populations. Seemingly in a state of shock, some of the audience, during the question period, asked questions or volunteered statements that were unscientific, unchivalrous, and embarrassing to the rest of us. Few could believe that a mere snake was that efficient a predator and could build up the numbers commensurate with such devastation.

Apparently after keeping a low profile in southern Guam through the 1950s and 1960s this nocturnal, tree-climbing snake suddenly expanded its population in the late 1970s. It hit the Air Force area in a wave. Electric outages due to snakes climbing into circuitry increased eight-fold in six years, and cost $13,000,000 between 1978 and 1982. Division personnel are now radio-tracking the snakes and have conducted feeding and baiting experiments that show the snake's great numbers in trees at night and its expertise at catching all sleeping birds. This just about fixes the entire blame upon the snake unless some still-to-be analyzed samples in Julie's elaborate series of disease experiments incriminate microorganisms as well. At any rate, the only hope for the remaining Guam endemic bats and birds seems to be captive breeding and removal to safety on nearby Bota.

Herewith is the latest word-of-mouth status of the birds:

Wedge-tailed Shearwater (*Puffinus pacificus chlororhynchus*).—Guam population long extinct.

Yellow Bittern (*Ixobrychus sinensis*).—Declining. The only native Guam bird that still maintains an island-wide distribution.

Mariana Mallard (*Anas oustaleti*).—Entire species became extinct in 1960s. Not a hybrid. The wrong picture in my article (Condor 51:204, 1949) may have encouraged this notion; the photo is of an Australian Gray Duck (*Anas superciliosa*).

Micronesian Megapode (*Megapodius laperouse laperouse*).—Disappeared from Guam before the 20th Century. Still common in the northern Marianas.

White-browed Rail (*Poliolimnas cinereus micronesiae*).—Guam population disappeared sometime during the 1960s or early 1970s.

Guam Rail (*Rallus owstoni*).—This flightless rail is an endemic species solely of Guam. It was granted emergency listing on the U.S. Endangered Species List on 11 April 1984 through the cooperation of the Division of Aquatic and Wildlife Resources (Department of Agriculture, Government of Guam), the Environmental Defense Fund, and the Departments of Interior and Defense. The emergency was occasioned by the intention of Andersen Air Force Base to clear the forest habitat of the last continuous breeding population of the Guam Rail. The Air Force has prepared an environmental impact statement and will eventually clear this area adjacent to an existing parking ramp. On 27 Aug. 1984 the bats and other birds from the original proposals of 1978 were entered on the U.S. Endangered Species List. A captive breeding program for the rail and other species was started at Guam, the Philadelphia and Bronx Zoos, the National Zoological Park, and, recently, the Denver Zoo; it is being coordinated by the American Association of Zoological Parks and Aquariums. The Guam Rail nests again as soon as its young are independent, so that captive breeding by the Division on Guam continues to be successful and several broods have been raised at the Smithsonian's Front Royal facility (National Zoological Park, Conservation and Research Center). The rails at the north end of the Air Force runway are still there but probably declining. The total population is no more than 100 birds.

Guam Gallinule (*Gallinula chloropus guami*).—Listed as endangered on 27 Aug. 1984; still holding its own in remaining marshes. Although it was named from Guam, this race of the Common Gallinule occurred or still occurs on other islands of the Marianas that support marshes.

White-throated Ground Dove (*Gallicolumba xanthonura xanthonura*).—About 500 in 1979; now uncommon at north end of island.

Mariana Fruit Dove (*Ptilinopus roseicapilla*).—Less than 300 in 1979, now very rare.

Vanikoro Swiftlet (*Aerodramus vanikorensis bartschi*).—Listed as endangered on 27 Aug. 1984. About 225 remain at an active breeding cave.

Guam Micronesian Kingfisher (*Halcyon cinnamomina cinnamomina*).—A unique subspecies found only on Guam, and the only population of Micronesian Kingfishers in the Marianas Islands. Listed on 27 Aug. 1984. About 25 pairs remain on Guam. Twenty-one sent to the United States have not yet bred. Printing errors in the table of my article (Condor 51:211, 1949) are corrected by removing the word "same" from the line pertaining to the juvenal plumage. I had no juveniles of *pelewensis* and *teraokai* for comparison.

Guam Broadbill (*Myiagra freycineti*)—A unique species of Guam. Listed as endangered on 27 Aug. 1984. Too rare for captive breeding. Last two seen March and Sept. 1984. Printing errors in my table (Condor 51:215, 1949) can be corrected by deleting the words "more salmon" from the bottom of the right-hand column on the line pertaining

to extent of white, and by adding "same as male" at the bottom of both female columns on the line pertaining to tone of orange.

Rufous-fronted Fantail (*Rhipidura rufifrons uraniae*).—There were two or three singing males in July 1984. Inadvertently left off list proposed for endangered status in 1978; now proposed and near extinction. Too rare for captive breeding.

Nightingale Reed-warbler (*Acrocephalus luscinia luscinia*).—Vanished in the 1960s when the marshes were drained and developed.

Guam Bridled White-eye (*Zosterops conspicillata conspicillata*).—A subspecies found only on Guam. Was too rare for captive breeding when listed as endangered on 27 Aug. 1984 and now extinct. A printing error in my table (Condor 51:217, 1949) can be corrected by adding the figure "8" to the line pertaining to immatures from Tinian, in the column for yellow base of lower mandible.

Cardinal Honeyeater (*Myzomela cardinalis saffordi*).—Confined to northern tip of island in 1981; very rare at present.

Micronesian Starling (*Aplonis opaca guami*).—Still occupies about one-tenth of original range but nowhere common.

Mariana Crow (*Corvus kubaryi*).—Found only on Guam and the neighboring island of Rota. Listed as endanged on 27 Aug. 1984. Now less than 100 remain on Guam.—Joe T. Marshall, *U.S. Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560.*

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ANNOUNCEMENTS

AMERICAN ORNITHOLOGISTS' UNION MEETING

The One Hundred and Third Stated Meeting will be held at Arizona State University in Tempe, Arizona, from 7–10 October 1985. All persons interested in the conservation and management of birds are encouraged to attend.

Call for papers to the membership will appear in April, with deadlines for program space being 15 June 1985 for the general scientific program. Non-AOU registration costs are the same as for members ($30 pre-August 1 for nonstudents and $20 for students with copies of validated ID's; $40 post-August 1 for nonstudents and $25 for students with copies of validated ID's).

A symposium on the biology and management of Bald Eagles is scheduled Monday, 7 October from 1:00 to 5:00 pm, but if participation interest in the symposium continues, the starting time will be 10:00 am, with notification. Deadline for manuscripts is 15 June 1985.

A symposium on avian olfaction will be held on Monday, 7 October from 1:00 to 5:00 pm. There will be seven to eight half-hour presentations of original research.

A symposium on the importance of competition in structuring avian communities will be held Tuesday, 8 October, from 9:00 am to 12:00 noon. The program will consist of two overview papers (Drs. Thomas Schoener and John A. Wiens) and field studies.

General scientific paper sessions will begin at 1:00 pm, Tuesday, October 8 and continue through Thursday, 10 October.

Workshops on use of visual aids in presenting scientific data, experimental methodologies and their use in scientific studies, and Bald Eagle color marking protocol will be held Monday, 7 October. Anyone desiring to present a workshop at these meetings, register as a nonmember, or wanting more information please contact:

Dr. Robert D. Ohmart
Center for Environmental Studies
Arizona State University
Tempe, Arizona 85287

FINAL ANNOUNCEMENT—
XIX CONGRESSUS INTERNATIONALIS ORNITHOLOGICUS

The 19th International Ornithological Congress will be held in Ottawa, Canada, from 22 to 29 June 1986. Its President is Prof. Dr. Klaus Immelmann. The scientific program has been determined and comprises plenary lectures, symposia, contributed papers (oral and poster), roundtable discussions, special-interest-group meetings, and workshops. Pre- and postcongress excursions and workshops are planned, as well as early-morning bird walks and other activities for members and those accompanying members.

The deadline for registration and submission of contributed papers is January 1986. Additional information, the final circular, and registration forms are available from:

Dr. Henri Ouellet
Secretary General
XIX Congressus Internationalis Ornithologicus
National Museum of Natural Sciences
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RAPTOR RESEARCH FOUNDATION CONFERENCE—NOVEMBER 1985 ANNOUNCEMENT AND FIRST CALL FOR PAPERS

The 1985 Raptor Research Foundation (RRF) International Meeting and Symposium on the Management of Birds of Prey will be held at the Capitol Plaza Holiday Inn in Sacramento, California, 2–20 November 1985. Highlights of the meeting will include (1) the Second RRF Conference on Raptor Conservation Techniques—Twelve Years of Progress, 1973–1985; (2) a Western Hemisphere Meeting of the World Working Group on Birds of Prey (ICBP); (3) the Second International Vulture Symposium; (4) a Western North America Osprey Symposium; (5) a Workshop on North American Candidate Endangered Raptors; (6) an International Symposium on Raptor Reintroduction; and (7) a Symposium on Raptor Rehabilitation, Captive Breeding, and Public Education. For more information, or if you are interested in presenting a paper, please contact Dr. Richard R. Olendorff, U.S. Bureau of Land Management, 2800 Cottage Way, Sacramento, California 95825, or Nancy Venizelos, San Francisco Zoological Society, Sloat Blvd. at the Pacific Ocean, San Francisco, California 94132.

JOINT MEETING OF THE PACIFIC SEABIRD GROUP AND THE COLONIAL WATERBIRD GROUP

A joint meeting of the Pacific Seabird Group and the Colonial Waterbird Group will be held 4–8 December at the Holiday Inn, San Francisco, CA. Two symposia will be held: "Recent Advances in Gull Research" and "The Use of Man-modified vs Natural Wetlands by Waterbirds and Seabirds." Paper sessions will be held 5–7 Dec., with field trips on the 8th. For information contact:

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HAWK MOUNTAIN SANCTUARY RESEARCH AWARD

The Hawk Mountain Sanctuary Association is accepting applications for its ninth annual award for raptor research. To apply for the $750 award, students should submit a brief description of their research program (maximum of 5 pp.), a curriculum vitae, and two letters of recommendation by 30 September 1985, to Stanley E. Senner, Executive Director, Hawk Mountain Sanctuary Association, Rt. 2, Pennsylvania 19529. The Association's board of directors will make a final decision late in 1985. Only students enrolled in a degree-granting institution are eligible; both undergraduate and graduate students may apply. The award will be granted on the basis of a project's potential to improve understanding of raptor biology and its ultimate relevance to conservation of North American raptor populations.

This issue of *The Wilson Bulletin* was published on 26 June 1985.

The Wilson Bulletin

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BEHAVIOR AND NESTING BIOLOGY OF THE ST. ANDREW VIREO

JON C. BARLOW AND STEPHEN V. NASH

The St. Andrew Vireo (*Vireo caribaeus*) is a little known species endemic to the tiny Caribbean Island of San Andrés (12°35′N, 81°42′W), Colombia. Bond (1950) reported that this species was common there during his visit in 1948. In 1972, however, Barlow found it in any numbers only in brushy pastureland and mangrove swamp in the southern third of the island—an area of ca 17 km^2. Only brief notes on prebreeding weight and testes size (Russell et al. 1979), song in males (Barlow 1981), and on general status of the population (Bond 1950, 1974; Paulsen et al. 1969) have been published.

Herein we report for the first time the discovery and appearance of the nest, eggs, and nestlings of this vireo, and we comment briefly on parental care of nestlings, other nest-associated behavior, territoriality, vocalizations, foraging behavior, and interactions with other avian species. The observations presented here were made by Barlow in April 1972 and by Nash in June 1983.

METHODS AND STUDY SITE

Barlow visited San Andrés between 6–12 April 1972, in the company of S. M. Russell and D. W. Lamm. The party spent 2 days (10–11 April) on nearby Providencia Island (13°22′N, 81°23′W) (Russell et al. 1979). The principal study area on San Andrés was west of the Caribbean Hotel, 1.6 km south of the town of San Luis. Nash visited the same site between 3 and 8 June 1983.

The trip in 1972 involved acquisition of voucher specimens, tape recording of vocalizations, and a qualitative assessment of habitat, foraging behavior, nesting activity, and territoriality. Nash emphasized recording of vocalizations, and searched for evidence of nesting.

←

The color frontispiece is a painting by John P. O'Neill of a St. Andrew Vireo (*Vireo caribaeus*) at a nest.

Crude estimates of the size of territories were based on distances individual singing males traversed in response to playback of song, and the density of singing males in the primary study-site—an area of ca 50 ha immediately west of the hotel. Interactions with syntopic species were also noted.

San Andrés is ca 13 km by 4 km and, although generally low-lying, the island has a central ridge (elev. 95 m) running along much of its long axis. The indigenous population in 1983 exceeded 30,000 persons, most of whom lived in the northern two-thirds of the island. The town of San Andrés is the center of the tourist-oriented north end, and little habitat for scrub-dwelling birds remains in the town or nearby. Both of us were struck by the paucity of birds in the urban area during our separate visits.

Much of the island is covered with coconut palms (*Cocos nucifera*), planted in the 19th century. Isolated groves of native trees, some reaching 20 m, are associated with inland mangrove swamps.

The area in which we made our observations was shrubby pasture dotted with palms, mango (*Mangifera indica*), and dense patches of evergreen scrub as much as 30 m in diameter and 8 m tall. Several shallow pools were present in 1983, but a prolonged drought was underway in 1972 and a single spring was the only source of fresh water in the study area. Barlow traveled over much of the island by car in 1972, and in 1983 Nash wandered widely on foot in the southern third of the island in search of vireos.

Although our observations were largely anecdotal, some behavioral events were witnessed often enough to allow comparison with patterns in other species of the subgenus *Vireo*. It became apparent that we encountered different stages of the breeding cycle of *V. caribaeus* in our separate visits, and accordingly, the vireos responded differently to playback and resource availability in April than in June.

RESULTS AND DISCUSSION

Territorial behavior.—Territories were no more than 0.5 ha in area where *V. caribaeus* was common. On 7 April 1972, 10 males, seemingly uniformly spaced, were heard singing in the shrubby pasture-site in an area of about 5 ha. On other occasions (9 April 1972, 3 June 1983) four singing males, again equally spaced, occupied part of the same area.

Twice (both on 9 April 1972) three males sang within 5 m of one another, seemingly at territorial boundaries. Vocal dueling was taped only once in 1972 (9 April) but noted 20 times. In territorial encounters, males sang within a few meters of each other, and on all occasions but one they sang different songs. In that one instance, two of three males matched songs after a few minutes of singing different ones.

Response by males to playback of just-recorded song in April 1972 was sometimes accompanied by partial erection of feathers of the thorax and tail-fanning. In one example, reaction by a male to playback was intense with the feathers of the thorax ruffled, the tail broadly fanned, and wings held out slightly from the body. This aggressive display closely resembled high intensity postures seen in Bell's (*V. bellii*) and White-eyed (*V. griseus*) vireos in response to conspecific intruders (Barlow 1962).

Foraging behavior.—*Vireo caribaeus* is the most active and energetic of any of 20 foliage-gleaning species of vireos previously seen by Barlow (1980, pers. obs.) in the field. In fact, it reminded him more of a wood

warbler (Parulinae) or a kinglet (*Regulus* sp.) than had any other vireo. However, no special adaptations in jaw musculature for rapid gleaning were found in *V. caribaeus* by Orenstein and Barlow (1981) that might distinguish it from eight other species of generalized foliage-gleaning members of the subgenus *Vireo*.

Foraging occurred from as low as a few centimeters above the ground to 5 m in shrubby vegetation and occasionally as high as 10 m in tall trees. Arthropods were usually gleaned from leaves and twigs by stalking; hovering at a leaf cluster was seen only once in 30 min of continuous observation of a foraging bird in April 1972. On 5 June 1983, Nash saw a male catch a small (ca 2.5 cm) green caterpillar in its beak and then bang the caterpillar against a twig before eating it. Striking of prey against a twig is a foraging tactic frequently seen in many other vireos (Barlow, pers. obs.). Most prey items were too small to be identified. We saw no fruit eaten in several hours of general foraging observations.

Vireo caribaeus males sang frequently as they foraged. Males and females uttered single-note contact calls as they foraged. This habit of singing and calling while foraging is wide-spread among the Vireonidae (Barlow 1962, Barlow and James 1975, James 1976).

Comparisons with V. altiloquus.—Thicket-foraging vireos (subgenus *Vireo*) are regularly syntopic with arboreal-foraging species of the subgenus *Vireosylva* in the West Indies. On San Andrés the uncommon Black-whiskered Vireo (*V. altiloquus canescens*) occurs with *V. caribaeus*. These two vireos are separated by size (*V. caribaeus,* 10 g [N = 1] vs *V. a. canescens*, 21.9 g [N = 1]) and ecologically by height in the canopy at which they center their foraging activities. *V. caribaeus* frequented foliage below 5 m in contrast with *V. a. canescens,* which foraged higher—between 5 and 10 m (N = 1 male, 1 female, ca 40 min total observation time in April 1972). This Black-whiskered Vireo also differed from *V. caribaeus* in the high incidence (40% of all observations) of fruit consumed; in slow, deliberate foraging pace; and in frequency of occurrence of hovering at leaf clusters (in 20% of foraging attempts).

Vocalizations.—The song of *V. caribaeus* will be described in detail elsewhere, but may be heard on phonodisc (Barlow 1981). Song in this species is unusual in comparison with other vireos because it comprises three distinct patterns, each of which closely resembles the predominant song pattern in other species in the subgenus *Vireo*. The three patterns of singing by *V. caribaeus* are distinguished from each other by the kinds of syllables uttered in any given song bout. The structurally simplest of these is "chatter" song in which the same syllable is repeated from 2–20 (or more) times. This song format is shared with most populations of the Mangrove Vireo (*V. pallens*) of southern Mexico and northern Central America, the Cozumel Vireo (*V. bairdi*) of Cozumel Island, Mexico, and

the Thick-billed Vireo (*V. crassirostris approximans*) of Providencia Island ca 77 km to the north of San Andrés. The second type consists of songs of two different syllables, each of which may be uttered serially 1–15 times. This pattern resembles that of the Jamaican White-eyed Vireo (*V. modestus*), and apparently also that of a population of the Mangrove Vireo (*V. p. semiflavus*) from Utila Island in the Bay of Honduras (Bond 1950). A second kind of polysyllabic song given by *V. caribaeus,* composed of three or more different syllables uttered in random order, is similar to the heterosyllabic song of all other "white-eyed" type vireos. All three of these song patterns are given by *V. caribaeus* in territorial contexts.

At least three calls have been identified in the repertoire of *V. caribaeus* including: (1) single notes uttered as adults forage together that are indistinguishable spectrographically from contact notes given by other "white-eyed" vireos; (2) a *chee chee* . . . heard in a variety of contexts in which agitation of some sort is evident, as when an observer is close to the nest; and (3) a "raspy-buzz" given in response to playback and emblematic of high intensity aggression. The last two calls resemble those of other "white-eyed" vireos (Barlow 1962). The paucity of calls described herein does not necessarily indicate a smaller repertoire of vocalizations by *V. caribaeus* in comparison to repertoire size of other "white-eyed" vireos, but rather that the call-note system has yet to receive adequate study.

After Barlow found no evidence of nesting activity and noted that three males had testes smaller than expected for full breeding condition (largest diameter 5 mm) in April 1972, it was assumed that breeding activities had not yet been initiated. Similarly in 1948 Bond (1950:48) saw no breeding activities in *V. caribaeus* in late April, leading him to predict that breeding in this species doubtless occurred in late May and early June during the first "rainy season" as with land birds in the Greater Antilles. In confirmation of this speculation, on 3 June 1983 Nash, attracted by the furtive behavior of a silent bird apparently paired with a singing male, discovered the first nest of *V. caribaeus* known to biologists. It was a pensile structure of typical vireonid construction (see Frontispiece) suspended 2 m above the ground from a fork on a small branch in a black mangrove (*Avicennia marina*), 4 m in height.

Nash located the nest when one of the birds (probably the female) landed on it. While sitting on the nest, the female gave agitation calls and the nearby male began to sing. Within a few moments the female flew off the nest, and the male flew into it. The male sang while on the nest. At one point during these observations, a Bananaquit (*Coereba flaveola*) flew close to the nest and was promptly chased away by the male vireo.

The nest contained two eggs, glossy-white in color with small brown

spots on the wide end, and with finer brownish specks sparsely distributed over the remaining surface. The two eggs measured 19 × 12.5 mm and 18 × 13 mm.

The nest comprised a cup decorated on the exterior with shredded, brownish-leaf mulch, occasional bits of pale greenish and feathery, mold-like moss, and had a lining of fine grasses. There were several dead leaves hanging from the bottom of the nest. The dimensions of the nest were: inside diameter 40 × 50 mm, outside diameter 50 × 60 mm, inside depth 45 mm, and external depth 60 mm. The habitat at this site was swampy, with large clumps of scrubby mangrove growth, interspersed with areas where many shoots of mangrove were emerging from the wet, muddy substrate.

Nash found a second nest, which contained two unfeathered young about 2 days old, on 4 June 1983, as he walked several dozen meters south of the first nest along a path through pasture in which grew scattered breadfruit (*Artocarpus altilis*) and mango trees. A silent *V. caribaeus* flushed but stayed nearby. Immediately Nash discovered the nest 1 m up suspended from a small terminal fork in a broad-leaved shrub (species identity unknown) 1.3 m in height. This second nest was a deep cup measuring: outside diameter 50 × 60 mm, inside diameter 35 × 40 mm, inside depth 40 mm, and external depth 70 mm. As with the first nest, leaves and other plant matter held together by moss fibers formed the exterior, and fine grasses lined the interior. Dead leaves also hung from the bottom of the cup. The dimensions of both nests resemble those of nests of *V. b. bellii* (Barlow 1962).

At site #2 the nest shrub was shaded by a large breadfruit tree. Cattle grazed in the pasture but rarely came near the nest-site. The soil was dry in contrast to the swampiness of the first nest-site.

The female at nest #2 gave a slightly agitated, buzzing call while the male sang in 3-note couplets. Otherwise the birds seemed relatively undisturbed by Nash's presence.

At nest #2 the young showed increasing motor control and activity on 5 and 6 June and were visibly more reactive to noise than on 4 June. On 5 June both nestlings gaped when the adults approached. On 5 June Nash watched feeding of nestlings for 30 min, but saw only two trips made to the nest by the adults. Both sexes brought arthropods to the nestlings. By 6 June feather tracts were darkened on the nestlings in nest #2, and primaries and secondaries of these young were beginning to emerge. On 8 June the young showed fast-developing pterylae, and their eyes were beginning to open.

On 7 June at noon, nest #1 contained two naked nestlings, with eyes closed. The female flushed from the nest and gave the buzzing call when

Nash approached. The young were smaller than those in nest #2 at the time of the discovery of that nest on 4 June. No eggshells were in evidence at nest #1, but Nash surmised that the young had hatched in the early morning of the 7th as the nest had contained two eggs on the 6th.

At the two nests both sexes sat on the eggs, brooded, and fed the young. This is the pattern of parental sharing typical of species of the subgenus *Vireo* (Barlow 1962), which contrasts in part with species of the Red-eyed Vireo (*V. olivaceus*—subgenus *Vireosylva*) species complex in which males do not sit on the eggs during the incubation period (Barlow and Rice 1977, Barlow 1985).

Systematic relationships to other subgenus Vireo *species.*—When species of Vireonidae are grouped according to patterns of behavior, the results parallel intrafamilial classifications based on standard morphometric and phenotypic characters (Barlow and James 1975; Barlow 1980, 1981) and phylogenetic relationships indicated by DNA-DNA hybridization studies (Sibley and Ahlquist 1982). No behavioral traits, useful in assessing systematic relationships among vireos, demonstrated by *V. caribaeus* were found to differ substantially in this species from traits already described in other scrub-dwelling species (Barlow 1962, Barlow and Rice 1977).

Of primary importance from a behavioral perspective in assessing systematic relationships of *V. caribaeus* to other vireos is the fact that the nest is typically pensile and closely resembles in construction all other known vireonid nests—a factor regarded as diagnostic of the Vireonidae by Barlow and James (1975). Likewise the eggs are quite similar in size, color, and pattern to those of other vireos. What is known of adult behavior during incubation reveals participation by both sexes in diurnal incubation duties and brooding of the young, traits shared by all vireos except those of the *V. olivaceus* superspecies group (Barlow 1985). The structure and type of vocalizations, and the foraging behavior, clearly ally *V. caribaeus* with other scrub-dwelling species. Taken in concert, the traits enumerated above indicate the close relationship of *V. caribaeus* to other West Indian and continental "white-eyed" vireos.

SUMMARY

The St. Andrew Vireo (*Vireo caribaeus*) endemic to San Andrés Island, Colombia, was studied in April 1972 and June 1983. Territories were as small as 0.5 ha in area and were located in mangrove swamp and open-scrub and pastureland habitats. Gleaning of arthropods from leaves and twigs was the predominant foraging tactic used by *V. caribaeus*. Most foraging was no higher than 5 m in broad-leaved trees and shrubs.

Song consisted of three basic types (one, two, and three or more syllable types per song) which closely resembled those of other "white-eyed" vireos. Only three kinds of call notes were heard: single contact notes, *chee-chee* agitation calls, and a high-intensity "buzz" associated with nest defense.

The nest of the St. Andrew Vireo, described for the first time, is of standard vireonid construction. The two eggs of the first described clutch were a glossy-white with brownish spots ringing the wide end, typical of scrub-dwelling vireos. A second nest contained the first observed nestlings, which closely resembled those of other vireos. Both sexes sat on the eggs during the day, and both adults brooded and fed the nestlings. Collectively behavioral traits of *V. caribaeus* suggest that it is closely allied to other species in the subgenus *Vireo* occurring in the West Indies.

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COLOR PLATE

The Frontispiece of a St. Andrew Vireo (*Vireo caribaeus*) at a nest has been made possible by an endowment established by George Miksch Sutton (1896–1982). The painting is by J. P. O'Neill.

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DISPLAY AND RELATED BEHAVIOR OF MALE PIN-TAILED MANAKINS

Barbara K. Snow and D. W. Snow

One of the most striking members of the highly endemic avifauna of the southeast Brazilian coastal forests is the Pin-tailed Manakin (*Ilicura militaris*). The species has been placed in a monotypic genus, and does not appear to be closely related to any other manakin. The bird is little known, apart from brief references to its display by Sick (1959, 1967), and its nest is undescribed. In this paper we describe the behavior of male Pin-tailed Manakins, and compare their displays with those of other manakin species.

METHODS

We studied the Pin-tailed Manakin in the Boracéia Forest Reserve, in the Serra do Mar about 80 km east of São Paulo, at an altitude of 850 m above sea level. Observations of males in their display territories totaled 44.5 h on 21 d between 14 November and 13 December 1983. We chose this period as it is at or near the height of the breeding season for most of the forest birds of southeastern Brazil. All detailed observations were made on four individual males, one of which was watched for 30-min periods in each hour throughout a complete day; the presence of seven other individuals was noted, but their displays were not recorded. Observations were made with 10× binoculars, usually at distances of 8–15 m. No blind was used, as the birds seemed unaffected by our presence. Tape recordings of their vocalizations were made with a Sony TC 800 B tape recorder and analyzed by sonagraph (Kay 6061B) and by Unigon Spectrum Analyser. Measurements of the elongated central tail feathers (see below) were taken from specimens in the São Paulo Museum of Zoology, University of São Paulo, Brazil.

APPEARANCE

The Pin-tailed Manakin is a typical small, sexually dimorphic manakin, with brightly colored adult male plumage and cryptic olive-green female and juvenile-male plumage. The adult male's upperparts are black, except for a patch of crimson feathers on the forehead, scarlet lower back and rump, and olive-green secondaries. The sides of the head and underparts are white to very pale gray. The iris is bright fawn-brown, and the legs and feet blackish. The central pair of tail feathers is pointed and project 21–25 mm beyond the others (N = 10). These feathers are only slightly elongated in females, usually projecting 2–6 mm beyond the others (N = 32; all 2–6 mm except for one of 7 mm); in juvenile males they tend to be longer, projecting 4–7 mm (N = 8; all 4–7 mm, except for one of 15 mm, this bird being in transitional plumage). Sick (1959) gives the mean weight (sex unspecified) as 13.5 g; an adult male trapped by us weighed

12.2 g. No geographical variation has been described in any part of the range, which extends from Espirito Santo south to Santa Catarina.

MALE TERRITORIES

We found adult males singing and displaying in undisturbed valley forest. On frequent visits to forested ridges, only 100–200 m higher, we found no Pin-tailed Manakins of either sex. Along a long-unused road, which ran for 1.5 km at a level of about 30 m above a small river through primary and old secondary forest, 11 male territories were found. The birds were in four groups consisting of 3, 3, 3, and 2 individuals close enough together for each to be in auditory contact with at least one other member of its group (judged by the fact that they responded to sounds made by their neighbors). Individual males occupied territories of variable shape, 20–30 m across; more exact measurement in most cases was hampered by the steep and broken terrain. The distance between the centers (position of the mating perch—see below) of the two contiguous territories watched most intensively was 37 m, and this seemed typical of the spacing of others less intensively watched. Groups of males were several hundred meters apart.

All the territories had abundant slender perches (5–10 mm diameter) at heights of 4–10 m, mainly side branches of understory trees and vine stems, on which the males spent most of their time, and from which they delivered their frequently repeated songs. In addition, each territory included a main display perch (in one case, two such perches), hereafter called the mating perch, used in the culminating phases of courtship display. The five mating perches examined were more or less horizontal sections, about one m long, of branches with a diameter of about 50 mm, much thicker than the other perches used. Three mating perches were the main stems of small trees that had collapsed partially and had continued to grow in a bent-over position; two were horizontal branches of larger trees. All were well below the forest canopy, their heights above ground ranging from 3.3 to about 13 m. In addition to being horizontal, they were without side branches and clear of entangling vegetation.

Attendance at the territory.—The males were present in their display territories for nearly the whole of the daylight hours. An all-day watch on one male, beginning at dawn and continuing with 30-min observation periods each hour until its activities ceased, showed that it began to display by singing at 05:40 (local time) and sang for most of the time between then and 17:35. It was present for at least 87% of the intervening observation periods. During other early-morning watches totaling 7.5 h, the males (N = 3) were present for 97% of the time.

We never saw males feeding or searching for food in their display territories, but one male fed regularly on fruit from a nearby tree (*Rapanea* sp., Myrsinaceae). His bouts of feeding were easy to record, as the tree was a sparsely foliaged emergent near the forest edge. Seven feeding bouts (timed from the bird's flying up into the tree until his departure from it) lasted for 20–47 sec ($\bar{x}$ = 36 sec), and 6–8 fruits were taken per visit (N = 5). This bird started to sing again within seconds of his diving down out of the feeding tree back to his display territory, and his appearance in the feeding tree followed usually within a minute of the end of a singing bout, so that he was absent from his territory for no longer than about 1.5 min. Periods when the other males were not heard and could not be seen in their display territories were taken to indicate foraging trips. These ranged from 1.5 to 3 min ($\bar{x}$ = 2.1 min, N = 7), suggesting that these birds traveled farther to obtain food.

"Gardening."—In the early morning, during the main peak of display (see below), the males regularly cleared their main perches of obstructing vegetation. This was seen on 11 occasions; all but once between 06:00 and 08:00, and mostly between or during bouts of display on the mating perch. "Gardening" consisted mainly of pulling or picking pieces out of leaves growing above the main display perch, or pulling at twigs, either from a perch or while flying. Males hovered for several seconds, hanging onto a leaf, with wings beating, in attempts to detach leaves or pick at them. Twice a male was seen pulling off small pieces of moss from the main perch. As a result of these activities, the upper side of the mating perch is kept clean of moss (and thus stood out from the surrounding moss-covered branches), and the air space above it is kept more or less clear of obstructions and thus suitable for the display jumps.

THE DISPLAY REPERTOIRE

Song.—Males in their display territories advertised their presence by means of a frequently repeated, simple song consisting of a series of downwardly inflected notes of characteristic form (Fig. 1a,d). Most songs consisted of 5–8 notes, each one slightly lower-pitched than the one before and the last note often fainter than the others. Each note spanned a wide range of frequencies, the first note of a song being usually between 7.8 and 6.7 kHz and the last note between 6.6 and 5.6 kHz. The descending series of downwardly inflected notes, ending faintly, sound plaintive to the human ear, and is very unlike the call of any other manakin with which we have been acquainted. Occasionally, much longer songs were given (Fig. 1d), the three recorded having 14–17 notes. In these longer songs, the pitch of successive notes descended in the usual way up to the

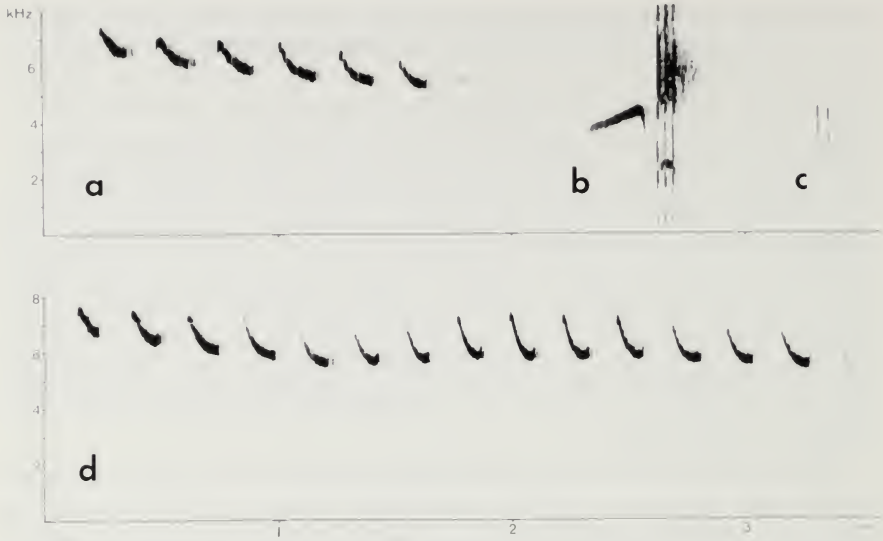

FIG. 1. Sounds associated with displays of male Pin-tailed Manakins (*Ilicura militaris*): (a) normal song, (b) the *weep* call, followed by a snap (made by wings, consisting of three pulses of sound) and a second, lower-pitched note synchronous with the snap, (c) click (made by wings, consisting of four pulses of sound), and (d) "long" song. Duration of calls in seconds.

fifth or sixth note, and then rose, giving the impression that the bird had begun to sing a second song before the first had ended.

While singing, males assumed a fluffed-out posture with the red rump feathers erected (Fig. 2a). This was strikingly different from the sleeked appearance characteristic of the other displays. All individuals watched used a large number of different song perches, mostly in the understory at heights of 6–9 m. At times when display activity was less frequent, they sometimes used higher perches, up to 14 m. Conversely, during periods of high activity, particularly during intrusions by young males, they tended to sing on low perches, sometimes less than 4 m high.

Songs were uttered at short intervals in the early morning with intervals lengthening and becoming less regular as the day went on. Thus one male sang at intervals averaging 11.5 sec (N = 98; SD = 2.31) between 06:00 and 07:00, 13.9 sec (N = 94; SD = 3.02) between 07:00 and 08:00, and 24.9 sec (N = 96, SD = 6.40) between 14:00 and 15:00. The male that was watched for a whole day sang 693 songs during the observation periods, so that its total output must have been of the order of 1400 songs.

Noisy flight.—Adult males in display territories flew silently or with a mechanical whirring sound that undoubtedly was made with the wings. The same whirring sound sometimes was also produced when males

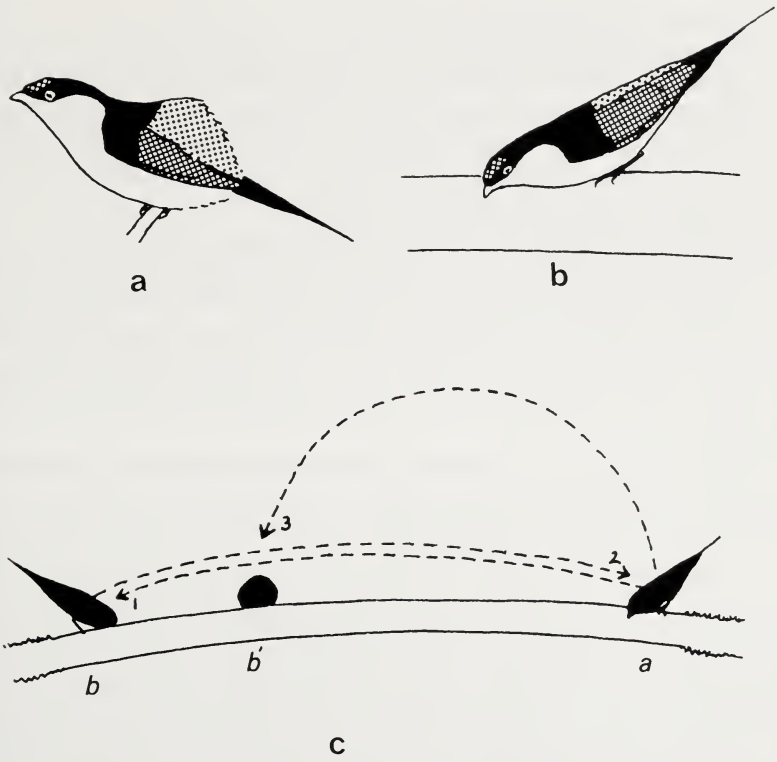

FIG. 2. Postures and displays of male Pin-tailed Manakins (*Ilicura militaris*): (a) singing male, with red feathers of lower back and rump conspicuously fluffed, (b) chin-down posture with plumage sleeked, preparatory to making a snap-jump along the mating perch, (c) sequence of jumps leading to mating. The male makes two snap-jumps over the crouching female, and then mounts with a third, semicircular jump.

jumped between adjacent perches. The change from silent to noisy flight occurred on the arrival of a female or young male in the adult male's territory. When the visitor arrived, the resident male usually flew straight to his mating perch. Thus, most flights to the mating perch were noisy, but noisy flights sometimes occurred elsewhere in the territory.

Single snap.—This display was performed everywhere in the display territory, including the mating perch. Twelve of 37 (32%) single snaps made by the male, whose activity was monitored throughout a whole day, were performed on or near the mating perch. Without adopting any obvious preparatory posture (i.e., from a normal perched position) the bird suddenly would take off with a loud snapping sound and would make a short flight in a curved trajectory to another perch about one m away or,

with a sharply angled trajectory, would return to another position on the perch from which it took off. Often, the snap was immediately preceded by a special call, *weep,* with an upward inflection, followed by a second note synchronous with the snap (Fig. 1b). Because it was swamped by the snap, we were unaware of the second note until we made the sonagrams. Rarely, a call that sounded identical to the *weep* was uttered by a male in its territory, unaccompanied by a snap.

An analysis of recordings of snaps showed that energy was more or less evenly distributed over a wide range of frequencies, with upper limits at 9.6–10.2 kHz and lower limits at 0.08–1.2 kHz. The sound consisted of three pulses separated by gaps of 0.033–0.035 sec, producing a rolling sound just detectable by the human ear. It was undoubtedly produced by the wings, but the wing movement was far too rapid to follow under field conditions.

Double snap-jump.—This display was usually performed on the mating perch (e.g., on 33 of 36 occasions recorded for the adult male most intensively watched). The male would position itself at one end of the cleared part of the perch, then, with plumage sleeked, would lower its breast and chin to the perch and raise its tail (Fig. 2b). A moment later it would jump, with a snap on taking off, and, with a low curved trajectory, would land at the other end of the perch, facing the way from which it came. The bird immediately would jump back with another snap, landing either on the mating perch, again facing the way from which it came, or on a higher perch near by. Double snap-jumps were seen at four different perches and the males were consistent in always starting at the same end of the perch. Only one male was seen to land on a higher perch after the jump back, probably because its mating perch was slightly sloping. The first jump was slightly uphill, so that the bird's trajectory on the jump back took it too high for a convenient landing on the mating perch.

The snaps made during the double snap-jump sounded no different from single snaps; those analyzed consisted of either 3 or 4 pulses of sound, separated by intervals of 0.032–0.035 sec. They were never heard to be preceded by the *weep* call.

Click display.—A faint click (Fig. 1c), audible only over a short distance and, like the snap, undoubtedly produced by the wings, was associated with various stereotyped movements. Sometimes the click display was simply a side-to-side pivoting accompanied by a click, first one way then the other, without changing perches, repeated up to a dozen times. Sometimes a click accompanied ritualized jumps, with sleeked plumage and an upright stance, along the mating perch or to and fro between the mating perch and perches above it. Finally, a click accompanied each jump made during the semicircular jump display, described below. Of 17 click displays

observed, 13 occurred on or near the mating perch; the others were performed from song perches in other parts of the display territory while female-plumaged manakins were perched above the displaying bird.

Recordings showed that clicks consisted of 1–4 pulses, weaker than the snap but with energy similarly distributed over a wide range of frequencies, the pulses being separated by intervals of 0.045 sec.

Semicircular jumps.—This display was only performed on the mating perch. In the chin-down posture with plumage sleeked (Fig. 2b), the bird would jump with a "click" along the perch, following a higher, more semicircular trajectory than in the snap-jump, and would land facing the way from which it came, and then make a similar jump back or, occasionally, to another perch. On all except one of the occasions when it was seen (N = 6; 2–8 jumps on each occasion), the first jump was from the same position on the mating perch as the first jump of the double snap-jump. Once the first jump of a double snap-jump was followed by a semicircular jump back. The semicircular jump was similar to the jump made by the male when it mounted the female, which was seen only once (see below).

RESPONSES OF ADULT MALES TO NEIGHBORS AND VISITORS

On 18 occasions, all between 06:55 and 08:50, birds in female-type plumage were seen visiting an adult male's display territory, usually flying to the mating perch or occasionally to other perches of similar thickness and orientation. On 13 of these occasions the visiting birds behaved as young males; they performed displays of adult-male type, but the mechanical sounds accompanying them were subdued. On the other five occasions the visitor's behavior suggested that it was a female; and one of these occasions culminated in mating. When a bird in female-juvenal plumage entered a male's territory, the male would sleek all his feathers, and they remained sleeked throughout the displays that followed.

Only once was another adult male seen inside a neighboring adult's display territory. On that occasion the latter was engaged in a long series of snap-jumps directed at an intruding young male. Though such trespassing was evidently rare, adult males regularly reacted to the sounds made by a neighbor. Frequently, when snaps were heard from a neighbor's territory, an adult male would at once fly to the edge of his territory abutting on his neighbor's and sing from that position before returning to the center of his territory.

Female visits.—The following was the initial sequence of events when the visitor was probably a female. At the arrival of a female above one of his song perches the male performed click displays on the song perch before flying with noisy flight to the mating perch, closely followed by the female. The male then moved to position *a* on the mating perch (Fig. 2c),

the position from which he took off for the first jump of a double snap-jump, and the female went to *b* or *b'*. The subsequent course of events leading to mating was seen only once, and was as follows. At 06:59 on 10 December, a female came to the male's mating perch. The male performed the click display 12 times, jumping between position *a* and some perches just above *b'*. While he displayed, the female watched him, and hopped a few times between positions *b* and *b'*, before perching across the branch at *b'*. The male then performed a double snap-jump over her and back, immediately followed by a semicircular jump straight onto her back. By this time the female was in a crouched position; during copulation the male gripped her crown feathers. After mating, the male left the mating perch and began singing almost immediately. The female left after a short preening bout. The whole sequence took just over a minute. Fifteen minutes later the male, followed by a female, returned to the mating perch. On this occasion the male made 18 click-display jumps from the mating perch to a perch just above, returning to the mating perch sometimes at position *a* and sometimes at *b*. The female appeared restless and hopped about more than in the previous sequence. Frequently, when the male landed at *a* he assumed a crouched chin-down presnap posture, only to abandon it and jump with a click back to the perch above. Eventually the male performed a double snap-jump over the female, but the latter did not crouch and both of them left without mating.

Visits by young males.—Presumed young males were seen on 13 occasions within an adult male's display territory. On 9 of these occasions they went to the adult's mating perch in his absence where they practiced single and double snap-jumps, semicircular jumps, and click displays. One individual sang briefly. Twice, two young males came together. Their displays were performed with sleeked plumage, and although the movements appeared identical to those of adult males, the snaps were faint and imperfect (perhaps due to their less modified wing feathers), and no clicks were audible. When performing the double snap-jump, they started from the same position on the perch as the resident male. On occasions when the adult male was present during visits by young males, there were confused interactions between owner and visitor(s), with click displays and noisy flights on and around the main mating perch, and with all birds in sleeked plumage. If a young male persistently tried to intrude and snap in an adult male's territory, the latter would fly with noisy flight between his song perches and chase the intruder with noisy flight. During one such intrusion, the adult male flew with noisy flight to perch just below a White-throated Spadebill (*Platyrinchus mystaceus*) and there made a few noisy hops from twig to twig, about 60 cm below the spadebill, perhaps mistaking it for the intruding manakin.

DISCUSSION

Our observations show that the Pin-tailed Manakin exhibits typical manakin courtship behavior, having a repertoire of striking, stereotyped postures and movements accompanied by vocal and mechanical sounds. These fulfill important functions in a polygamous mating system in which contact between the two sexes is brief: (1) to attract females to a fixed area by auditory and visual signals; (2) once a female is in the display territory, to indicate the mating perch (by flying to it with noisy flight and displaying there); and (3) to identify the exact position where the female must perch for copulation to be achieved. In their spatial organization, with small groups of males holding adjacent territories in what might be termed "exploded leks," the Pin-tailed Manakins studied by us resembled several other species of manakins, e.g., the Crimson-hooded Manakin (*Pipra aureola*) and the Tiny Tyrant-manakin (*Tyranneutes virescens*) (Snow 1963), and the Blue-crowned Manakin (*Pipra coronata*) (Skutch 1969). This does not exclude the possibility, however, that where Pin-tailed Manakin populations are denser, males may have their display territories closer together. Sick (1967) mentions that he often saw two or three male Pin-tailed Manakins in adjacent trees.

Some elements of the Pin-tailed Manakin's display are similar to elements of the display of other genera. The snap-jump resembles that of *Manacus,* but *Ilicura* differs from *Manacus* in using a horizontal rather than a vertical perch. Although the mechanical wing-noises resemble those made by *Manacus, Ilicura* does not show the modification to the secondary feathers seen in *Manacus,* which are apparently used in making the snap, nor does it have thin, stiff outer primaries, which in *Manacus* are almost certainly responsible for the grasshopper-like whirr made in flight. In fact the outer primaries of *Ilicura* are unusually broad at the distal end and narrow at the base. Whereas a whirring sound is always made by an adult male *Manacus* in flight (except during molt of its outer primaries; Snow 1962), male Pin-tailed Manakins evidently can control the production of the sound, indicating that a different mechanism is involved. The most obvious structural modification in *Ilicura,* the elongated central tail feathers, is found elsewhere in the manakins only in *Chiroxiphia,* which also shares with *Ilicura* a red crown patch and performs jumping displays on a horizontal perch (Snow 1963). It is evident that, based on courtship behavior, it is not yet possible to reach any conclusion as to the relationships of *Ilicura* within the family.

SUMMARY

We report observations made in November and December 1983 on the display of the Pin-tailed Manakin (*Ilicura militaris*), a southeast Brazilian endemic genus. Groups of 2–

3 adult males held contiguous display territories, each of which contained a special mating perch. Most displays were performed on or around the mating perch, which was kept clear of encroaching and epiphytic vegetation by regular "gardening." Males advertised their presence in their territories by repeated songs, given at short intervals throughout the day. A repertoire of stereotyped displays served to attract females to the mating perch, mating itself being preceded by ritualized jumps over the female and back. Elements of the courtship displays of the Pin-tailed Manakin resemble those of other manakins, but its relationships within the family are obscure.

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SPERM RELEASE IN MIGRATING WOOD-WARBLERS (PARULINAE) NESTING AT HIGHER LATITUDES

W. B. Quay

Although there are many descriptions of behavioral and ecological differences and adaptations among species of wood-warblers (Parulinae) (e.g., Lawrence 1948, 1953; Ficken and Ficken 1965, 1967; Kammeraad 1966; Meanley 1969, 1972; Welsh 1971; Stewart 1973; Thompson 1977; Sealy 1979; Moore 1980), very little has been published concerning differences in their reproductive physiology and chronobiology.

I report here the results of a study on the timing of sperm release in spring migrant warblers while they are still south of their known breeding ranges. These results are considered significant because they demonstrate (1) a hitherto unreported adaptation in some warblers to short nesting seasons at higher latitudes, and (2) the successful application of the cloacal lavage technique (Quay 1984) for ascertaining the timing of spontaneous sperm release in free-living passerine birds.

METHODS

Study sites and times.—Two sites were used in the collection of data and cloacal lavage samples for study. The first was a residential yard at the NE end of the city of Galveston, Galveston Co., Texas (29°19′N, 94°48′W). This site was 1.6 km NW from the Gulf of Mexico and was known for passage of large numbers of warblers and other passerines during spring migrations. Birds were mist-netted at least several days per week throughout most of 1982. Migrant warblers were captured from 20 March to 13 May 1982, with the largest numbers in the last week of April and the first week of May. One hundred and nineteen warblers representing 25 species were captured and studied at this site.

The second site was a farm about 5 km NNW from the town of Foley, Lincoln Co., Missouri (39°08′N, 90°46′W). The site was located on the western bluffs of the Mississippi River Valley, and possessed a diversity of habitats that were sampled with mist-nets from 30 April to 7 May 1983, and 1 to 14 May 1984. One hundred and eighty-one warblers representing 18 species were captured and studied at this site.

Species groups.—The 300 individuals and 29 species used in this study were arranged latitudinally and categorized according to two groups. The first of these, designated "mid-latitude nesters," contains the 14 species whose nesting ranges either include the Foley site (species numbers 1–13) (Table 1) or are south of it (species 14) (Table 1). These species are listed in Table 1 in the order of the approximate latitude of the center of their geographic nesting range within the general north-south zone occupied by the two study sites. The boundaries and centers of nesting ranges were calculated chiefly from the maps in Peterson (1980) with finer detail in relation to the Galveston site calculated from data in Oberholser (1974). The second of the two artificial species groups, designated "highlatitude nesters," contains the 15 species whose nesting ranges are north of both of the study sites. The arrangement of these species in Table 2 was by the same criterion employed in Table 1. These arrangements of warbler species by latitude, and the designation of distances in relation

TABLE 1

NESTING DISTRIBUTIONS AND CLOACAL SPERM IN MIDLATITUDE-NESTING WARBLERS ARRANGED BY LATITUDINAL CENTER OF NESTING RANGE

Species	Number examined	Latitudinal center of breeding range	Distance from Galveston to center/southern edge of breeding range (km)	Proportions of birds with cloacal sperm					
				Galveston, Texas			Foley, Missouri		
				♂	♀	Unk.	♂	♀	Unk.
1. Yellow Warbler (*Dendroica petechia*)	2	47°	2010/770	0/1	0/1	0/0	0/0	0/0	0/0
2. Ovenbird (*Seiurus aurocapillus*)	26	44°	1620/560	0/1	0/0	0/8	0/2	0/1	1/14
3. Black-and-white Warbler (*Mniotilta varia*)	12	42°	1460/140	0/5	0/3	0/0	0/3	0/1	0/0
4. American Redstart (*Setophaga ruticilla*)	10	42°	1460/140	0/2	0/4	0/0	0/2	0/2	0/0
5. Blue-winged Warbler (*Vermivora pinus*)	1	41°	1430/710	0/0	0/1	0/0	0/0	0/0	0/0
6. Northern Parula (*Parula americana*)	1	40°	1360/60	0/1	0/0	0/0	0/0	0/0	0/0
7. Louisiana Waterthrush (*Seiurus motacilla*)	3	38°	960/160	0/0	0/0	0/3	0/0	0/0	0/0
8. Worm-eating Warbler (*Helmitheros vermivorus*)	3	37°	930/200	0/0	0/0	0/3	0/0	0/0	0/0

TABLE 1
CONTINUED

Species	Number examined	Latitudinal center of breeding range	Distance from Galveston to center/ southern edge of breeding range (km)	Proportions of birds with cloacal sperm					
				Galveston, Texas			Foley, Missouri		
				♂	♀	Unk.	♂	♀	Unk.
9. Prothonotary Warbler (*Protonotaria citrea*)	11	37°	820/60	0/6	0/4	0/0	0/1	0/0	0/0
10. Kentucky Warbler (*Oporornis formosus*)	21	36°	750/170	0/1	0/6	0/1	8/10	0/2	0/1
11. Common Yellowthroat (*Geothlypis trichas*)	24	36°	Nesting range extends south of Galveston	0/6	0/4	0/0	6/9	0/5	0/0
12. Hooded Warbler (*Wilsonia citrina*)	7	36°	730/200	0/3	0/4	0/0	0/0	0/0	0/0
13. Yellow-breasted Chat (*Icteria virens*)	10	35°	Nesting range extends south of Galveston	0/0	0/0	0/3	3/5	0/0	0/2
14. Swainson's Warbler (*Limnothlypis swainsonii*)	1	34°	500/150	0/0	0/0	0/1	0/0	0/0	0/0
Totals	132				0/72			18/60	

TABLE 2

NESTING DISTRIBUTIONS AND CLOACAL SPERM IN HIGHLATITUDE-NESTING WARBLERS ARRANGED BY LATITUDINAL CENTER OF NESTING RANGE

Species	Number examined	Latitudinal center of breeding range	Distance from Foley site to center/southern edge of breeding range (km)	Proportions of birds with cloacal sperm					
				Galveston, Texas			Foley, Missouri		
				♂	♀	Unk.	♂	♀	Unk.
1. Blackpoll Warbler (*Dendroica striata*)	5	55°	1900/1490	0/2	0/0	0/0	0/2	1/1	0/0
2. Wilson's Warbler (*Wilsonia pusilla*)	2	53°	1580/1071	0/0	0/0	0/0	0/2	0/0	0/0
3. Tennessee Warbler (*Vermivora peregrina*)	23	53°	1520/890	0/9	0/9	0/0	2/4	0/1	0/0
4. Palm Warbler (*D. palmarum*)	19	52°	1440/800	0/0	0/0	0/0	0/4	0/0	5/15
5. Yellow-rumped Warbler (*D. coronata*)	74	52°	1430/780	0/0	0/1	0/0	0/37	0/15	0/21
6. Northern Waterthrush (*Seiurus noveboracensis*)	14	52°	1420/580	0/0	0/0	0/9	0/0	0/0	0/5
7. Magnolia Warbler (*D. magnolia*)	4	50°	1290/810	0/4	0/0	0/0	0/0	0/0	0/0
8. Black-throated Green Warbler (*D. virens*)	3	49°	1180/800	0/0	0/1	0/0	0/2	0/0	0/0

TABLE 2
CONTINUED

Species	Number examined	Latitudinal center of breeding range	Distance from Foley site to center/southern edge of breeding range (km)	Proportions of birds with cloacal sperm					
				Galveston, Texas			Foley, Missouri		
				♂	♀	Unk.	♂	♀	Unk.
9. Cape May Warbler (*D. tigrina*)	2	49°	1180/820	0/1	0/1	0/0	0/0	0/0	0/0
10. Bay-breasted Warbler (*D. castanea*)	5	49°	1150/940	0/5	0/0	0/0	0/0	0/0	0/0
11. Nashville Warbler (*V. ruficapilla*)	7	49°	1130/640	0/0	0/0	0/0	3/5	0/0	1/2
12. Canada Warbler (*W. canadensis*)	2	49°	1130/630	0/1	0/0	0/0	0/0	0/1	0/0
13. Blackburnian Warbler (*D. fusca*)	1	49°	1090/780	0/1	0/0	0/0	0/0	0/0	0/0
14. Mourning Warbler (*Oporornis philadelphia*)	4	48°	1000/400	0/1	0/0	0/0	0/3	0/0	0/0
15. Chestnut-sided Warbler (*D. pensylvanica*)	3	47°	880/550	0/1	0/0	0/1	0/1	0/0	0/0
Totals	168				0/47			12/121	

TABLE 3

CORRESPONDENCE OF CLOACAL SPERM INDEX (CSI) WITH SPERM NUMBERS PER MICROSCOPIC FIELD AND PER LAVAGE

CSI	Sperm/field	Sperm/lavage
0	0	0
1.0	0.00004	1–10
1.5	0.0125	1.5×10^3
2.0	0.5	6.0×10^4
2.5	2.0	2.4×10^5
3.0	5.0	6.0×10^5
3.5	12.5	1.5×10^6
4.0	33.0	4.0×10^6

to latitude, are approximations for comparative purposes only. The original data upon which they are based are fragmentary, and only parts of the total nesting ranges are involved in the calculations and the characterizations of nesting distributions.

Cloacal lavage specimens.—One or more (usually two) cloacal lavage specimens were taken from each bird within one hour of capture by mist-netting and prior to banding and release (Quay 1984). Disposable plastic pipette tips (Cat. No. OME 1–100, Orthomedics Inc., P.O. Box 247, Riverside, Connecticut 06878) were fitted with rubber bulbs and used to wash aliquots of about 0.05 ml distilled or deionized water in and out of the cloaca several times. The lavage (=wash) sample or specimen was then deposited on a clean 1 × 3 in. glass slide. This was immediately labeled with a diamond pencil, rapidly air-dried, and then stored in a dust-proof plastic slide box. Each pipette tip was discarded after a single use. The lavages were taken with minimal stimulation or trauma to the bird. Confirmatory evidence of this is provided by a male Kentucky Warbler that at the Foley site was first captured and lavaged in 1983 and was recaptured and relavaged three times in May 1984 without any signs of problems nor of notable reduction in sperm numbers per lavage.

Quantitative methods.—Quantitative evaluation of the dried cloacal lavages (CLs) was done on a Leitz Laborlux 12 microscope with phase contrast optics. The very refractile acrosomal region of the sperm, which glistened under phase contrast, was used as the feature upon which sperm counts were based. A "cloacal sperm index" (CSI) was determined from the average number of sperm per microscopic field (10× ocular, 40× objective lens). With the lavage area on each slide being of a standard size, an estimate of total number of sperm per lavage was made. The general accuracy and consistency of the CSI technique was checked by means of more detailed counts of sperm within microscopic fields at arbitrary intervals in a grid-like array over the entire lavage area (Table 3). The order of magnitude of numbers of sperm per lavage in males, as expressed by the CSI, is an indicator of level of sperm release. This is supported by results from several other kinds of studies on cloacal lavages of passerine birds (Quay, unpubl. data). Sperm release into the male cloaca in both resident and migrant warblers usually represents "spontaneous emission(s)" such as have been studied frequently in mammals (Orbach 1961, Lino et al. 1967, Fernández-Collazo et al. 1971) but rarely in birds (Reviers 1975; Quay, unpubl. data). Stimulated ejaculation, as in attempted as well as completed copulations, might also contribute to the sperm taken in avian cloacal lavages; however, I have found that male passerines isolated from females still have continuous emission of sperm into the cloaca. Unfortunately there is no technique available as

yet for distinguishing cloacal sperm samples having this mode of release as compared with ejaculation during copulation. In females, however, all cloacal sperm under natural conditions must originate through inseminations by males.

RESULTS AND DISCUSSION

Recognition of sperm. —Recognition of sperm on slides containing dried CLs was a problem only when an excess of large particulate fecal material was present. Dilution with the lavage water and use of small-tipped pipette tips usually circumvented this problem. In nonstained and noncovered CLs sperm could be readily identified and photographed with phase-contrast microscopy (Fig. 1). Sperm can be distinguished easily from other fibrillar inclusions of the CLs by their unique morphology and refractile characteristics. Warbler sperm, like those of other examined passerines (Nicander 1970, Lake 1981), have a helical or spiraling sheath that extends over much of the length of the tail.

Sperm in midlatitude nesters. —Table 1 summarizes the results for cloacal sperm in midlatitude nesters, and gives the latitudinal characteristics of the species in this group. The four warbler species in which cloacal sperm were found were within their geographic nesting range, and individuals of these appeared to be actively territorial during the sampling period at the Foley study area. All sexually determinable (chiefly by plumage and cloacal regional characteristics) individuals having sperm were males; males outnumbered females at this time in the early phase of the breeding season. Midlatitude nesters not showing sperm at Foley in May were few. At Galveston, on the other hand, none of the midlatitude nesters showed cloacal sperm. The species represented here consisted of some that have nesting ranges with southern limits 60 to 770 km to the north (species 1–10, 12 and 14) (Table 1), and others that nest through Galveston's latitude but did not appear to have territories near the study site (species 11 and 13) (Table 1). Therefore, none of the migrant midlatitude warblers at Galveston had cloacal sperm, even though some of these were within a short distance of their known nesting ranges. This was most clear for species represented by larger samples containing males (Black-and-white and Prothonotary warblers and Common Yellow-throat) (Table 1).

Sperm in highlatitude nesters. —Table 2 summarizes the results for cloacal sperm in highlatitude nesters, and gives the latitudinal characteristics of the species in this group. None of these species showed sperm at Galveston at any time through the spring migration period, but four did at Foley. The southern or nearest limits of the nesting ranges of these four are about 640 to 1490 km to the north of Foley. These warblers, therefore, were certainly migrants far from their eventual nesting territories when they were releasing sperm into the cloaca. Most of the individuals were

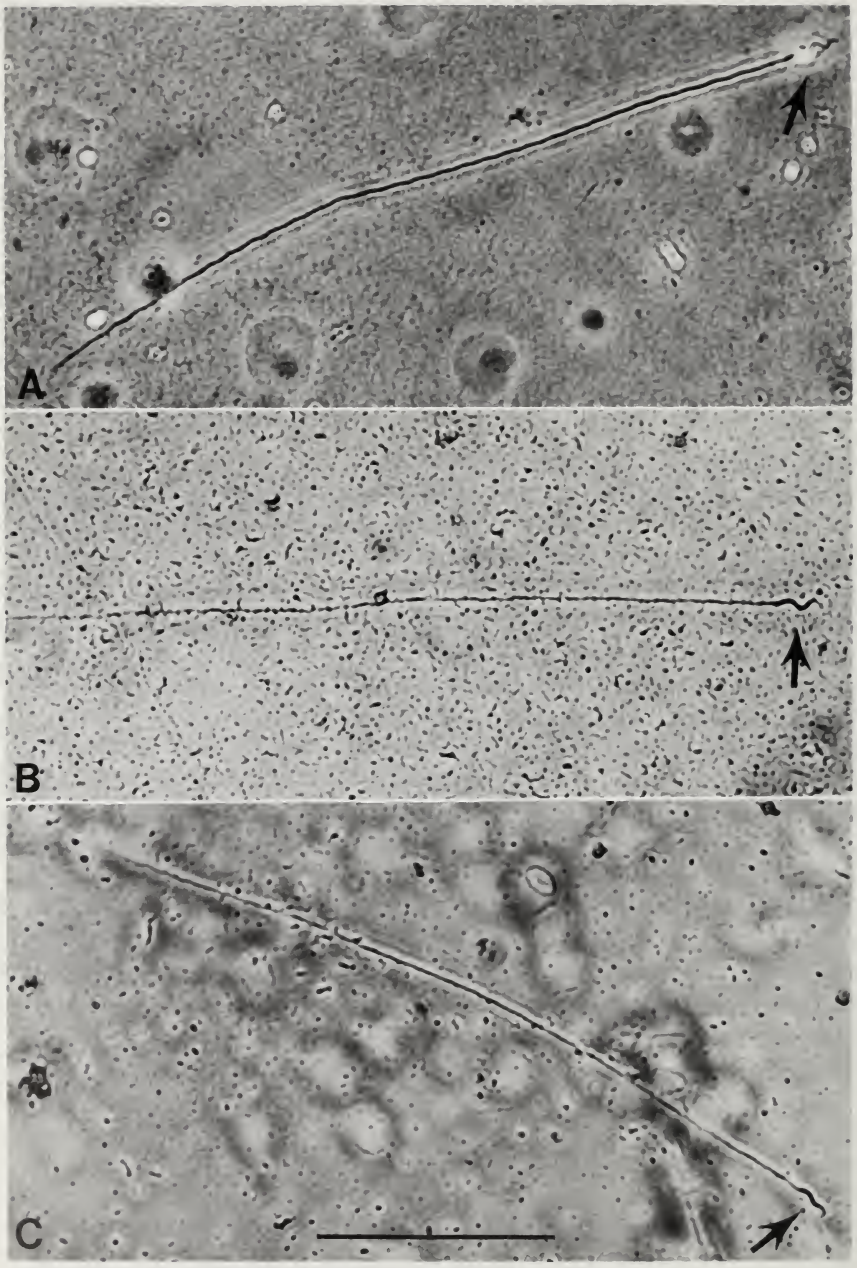

FIG. 1. Nonstained spermatozoa of spring migrant wood-warblers at Foley, Missouri, photographed with phase contrast microscopy. The head of each sperm is at the right

identifiable as males, or, lacking evident dimorphism externally, as sexual unknowns. The single Blackpoll Warbler having sperm was by external characteristics a female; however, it is probably premature at this time to accept this single occurrence as significant evidence of insemination prior to arrival at the nesting territory without either more definitive evidence of the bird's sex or additional examples from more samples. Nevertheless, Roberts (1936) has noted that "apparently mated pairs" of Blackpoll Warblers have been observed south of the known nesting range well into June.

It is significant that although Yellow-rumped (Myrtle) Warblers were the most numerous and most frequently sampled highlatitude migrant warblers at Foley, none had cloacal sperm. This is in marked contrast to the situation observed in Blackpoll, Tennessee, Palm, and Nashville warblers at the same site (Table 2). Thus, the data suggest that at least in several of the highlatitude nesters, and in none of the midlatitude nesters, there are species differences in the presence or absence of sperm release during spring migration (Tables 1 and 2). It is likely that precocious capacity for sperm release signifies an earlier physiological readiness for breeding. The actual occurrence of such breeding of course may depend upon ecological and behavioral factors as well.

Precocious physiological ability for breeding in spring migrants probably represents a component in adaptive strategies for reproductive success in the brief northern nesting season. Data in the literature on warbler reproduction, especially those concerning the timing of its phases and times of arrival and departure, allow some tentative suggestions about these adaptive strategies among warblers nesting at high latitudes. These birds are single-brooded in contrast with at least a few of the midlatitude nesters (e.g., Prothonotary and Swainson's warblers) that have been characterized as "sometimes" or "possibly" double-brooded (Harrison 1978). Additionally, the brevity of the northern nesting season is especially important for the Blackpoll Warbler, which is one of the last warblers to move to nesting grounds in the spring and which migrates from 4000 to 8000 km at that time (Bent 1953). As a group, the four northern species with cloacal sperm at Foley spend less time on their breeding/nesting range than does the Yellow-rumped Warbler (Table 4). In fact, similar available data for thirteen northern warbler species show that Blackpoll

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←

(arrows); the tail extends to the left. (A) Male Tennessee Warbler at 15:00, 11 May. (B) Sexually indeterminate Nashville Warbler at 19:00, 6 May. (C) "Female" (sexed by external characteristics) Blackpoll Warbler at 10:00, 13 May. All at same magnification; the bar scale is 20 μm long.

TABLE 4

TIMES SPENT ON THE BREEDING/NESTING RANGE BY HIGHLATITUDE SPECIES[a]

Species	Mean days from early spring arrival at breeding/nesting range to fall:	
	Early arrival south of breeding/nesting range	Late departure from breeding/nesting range
Blackpoll Warbler	90	101
Tennessee Warbler	98	128
Nashville Warbler	108	168
Palm Warbler	113	162
Yellow-rumped Warbler	143	192

[a] Based on data from Bent (1953).

and Yellow-rumped warblers represent the two extremes in the range of times spent in the respective breeding/nesting areas.

Comparisons of the characteristics of breeding/nesting timing in northern warblers (Table 5) provides evidence of different adaptive strategies. In this table I have chosen six highlatitude-nesting species, the four releasing sperm at Foley, and the two not releasing sperm there but represented by the largest sample sizes for such species. Palm and Nashville warblers are the species whose arrival and early egg-laying dates are most compatible with the possibility of breeding before arrival at the nesting site (Table 5). There is, however, an unintentional bias in the "mean days from SRF" (sperm release at Foley), as other information suggests that passage through the Foley region by these species probably started before May and that my samples may therefore be skewed toward the later migration time. An analogous situation certainly affects the representations of timing by the Yellow-rumped Warblers in Table 5. On the other hand, a bias in the opposite direction may possibly occur in the representations of timing by Tennessee and Blackpoll warblers, as my samples may have missed late migrants or stragglers. In spite of these possible biases in my sampling, the differences between "earliest eggs" and "early arrival" dates support belief in a dichotomy between Palm and Nashville warblers on the one hand and Tennessee and Blackpoll warblers on the other, in their adaptive strategies. The differences between "earliest eggs" and "early arrival" are 8 to 9 days for the former and 21 to 22 for the latter (Table 5). The comparable differences are 8 and 37 days for Northern Waterthrush and Yellow-rumped Warbler, respectively (Table 5). The extent to which early physiological preparedness for breeding is part of the adaptive strategy for particular northern migrant species or populations can be determined only with the aid of additional kinds of studies.

TABLE 5

TIMING OF BREEDING/NESTING IN RELATION TO MIGRANT PRESENCE AND SPERM RELEASE AT FOLEY (SRF)

Species	Dates of		At breeding/nesting range[a]				
			Earliest eggs		Mean early arrival		Duration of nesting cycle (days)
	Sperm release	Species present	Mean days from SRF	Dates	Mean days from SRF	Dates	
Releasing sperm at Foley							
Palm Warbler	5–7 May	1–9 May	0	6 May	−9	27 April	24
Nashville Warbler	5–9 May	2–11 May	0	7 May	−8	29 April	22–23
Tennessee Warbler	7–11 May	7–13 May	23	1 June	2	11 May	Unk.
Blackpoll Warbler	13 May	4–14 May	28	10 June	6	19 May	21–22
Not releasing sperm at Foley			Mean days from Foley	Dates	Mean days from Foley	Dates	
Yellow-rumped Warbler	—	→9 May	21	26 May	−16	19 April	24–27
Northern Waterthrush	—	→9 May	19	25 May	11	17 May	Unk.

[a] Based on data from Bent (1953) and Harrison (1978).

The new findings in the present report open to view the hitherto unappreciated possibility that there are functionally important species differences in the timing of sperm release in relation to migration and the nominal start of the breeding/nesting season.

SUMMARY

Cloacal lavages (washes) were taken from 300 wood-warblers representing 29 species. Birds were captured at Galveston, Texas, and Foley, Missouri, in the course of spring banding studies. Phase-contrast microscopy was used to determine occurrence and numbers of spermatozoa on the lavage slides. Cloacal release of sperm at Foley occurred in four species of warblers that were within their geographic nesting ranges (Ovenbird, *Seiurus aurocapillus*; Kentucky Warbler, *Oporornis formosus*; Common Yellowthroat, *Geothlypis trichas*; and Yellow-breasted Chat, *Icteria virens*) and in four species that were still far south (>640 to 1490 km) of their nesting ranges (Tennessee, *Vermivora peregrina*; Nashville, *V. ruficapilla*; Palm, *Dendroica palmarum*; and Blackpoll, *D. striata*; warblers). None of the midlatitude-nesting species had cloacal sperm while passing through Galveston as spring migrants. The four highlatitude-nesting species with cloacal sperm at Foley spend less time on their northern breeding range than do Yellow-rumped Warblers (*D. coronata*), the most abundant non-sperm-releasing migrant warbler at Foley. Precocious sperm release during spring migration in some highlatitude-nesting species is probably an adaptation for more rapid onset of reproduction in areas with short summers and associated ecological limitations.

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MOLT MIGRATION OF LARGE CANADA GEESE ON THE WEST COAST OF HUDSON BAY

Rolph A. Davis, Rene N. Jones, Charles D. MacInnes, and Allan J. Pakulak[a]

Nonbreeding segments of some waterfowl populations migrate northward from their breeding grounds to undergo summer molt (Salomonsen 1968). Several authors have documented molting areas of the "large" races of Canada Geese (*Branta canadensis*) in the Northwest Territories (Kuyt 1962, 1966; Hanson 1965; Sterling and Dzubin 1967). Although the relationship of the molting to the breeding ranges of the populations involved has been discussed, there is little information on the actual migration. Here we present data on the northward molt migration of large Canada geese along the west coast of Hudson Bay at the mouth of the McConnell River, with some comparative data from the Churchill area of Manitoba, and discuss the origin and destination of the birds involved. The races involved are *B. c. interior* and *moffitti,* sensu Palmer (1976), who included *maxima* in *moffitti.* Although the name "*maxima*" is commonly used in the literature, we follow Palmer as the most recently published authority.

METHODS

We observed molt migration of large geese during extensive studies of "small" Canada Geese (*B. c. hutchinsii-parvipes* complex, MacInnes 1966) nesting at the mouth of the McConnell River (60°50′N, 94°25′W; MacInnes et al. 1974). Migrating large geese were easily distinguished from residents by their larger size, distinctive voice, and slower wing beat.

Observations on nesting small Canadas took place daily during May through August. Casual observations of the molt migration of large geese were made during these months in 1959–60 and 1964–68, including recording the first and last dates and peak periods of migration. Systematic observations in 1969 and, to a lesser extent, 1970, allowed estimates of total numbers to be made. Additional observations were made by C. D. Ankney in 1971, and by Pakulak from 1967 to 1970 in the Churchill area (58°45′N, 94°5′W) about 250 km south of the McConnell River.

In 1969, the senior author was engaged in intensive study of loons, primarily from an elevated live-in blind, and was able to make nearly continuous observations of migrating large geese over a strip of Hudson Bay coast about 8 km wide. Loud, distinctive calls of flocks passing over drew attention to them, and normally the observer was able to make a count. During periods when actual counts were not taken, estimates were made based on daily impressions of overall volume, incidental counts by three other observers, and the volume in preceding and following counts. Estimates of total numbers were compiled for

[a] Allan Pakulak died in a helicopter crash in 1972. He contributed actively to this paper before that event.

TABLE 1

CHRONOLOGY OF MOLT MIGRATION OF LARGE CANADA GEESE AT THE MCCONNELL RIVER, NORTHWEST TERRITORIES, CANADA

Year	First flocks	Period of peak migration	Last northbound flocks
1959	23 June	23–26 June	3 July
1960	19 June	22–28 June	5 July
1964	18 June	23–25 June	8 July
1965	18 June	22–27 June	27 June
1966	18 June	26–29 June	2 July
1967	19 June	29 June–2 July	22 July
1968	16 June	25–28 June	28 June
1969	17 June	21–26 June	27 July
1970	12 June	25–30 June	11 July
1971	9 June	16–26 June	13 July

07:00–24:00 of each day in the migration period (17 June–27 July) (Table 1). Actual counts were most frequent on the days of heaviest passage, and were well spread over the day. Pakulak's counts at Cape Churchill were made in a similar manner, also during extensive daily field work, but he covered only a 4-km wide area, and made no estimates beyond his actual counts.

Directions taken by flying birds were noted in 1969, and flight elevation was estimated for a sample of 3077 geese during 21–24 June. Three categories were recognized: low (<30 m), medium (30–150 m), and high (>150 m).

RESULTS

Chronology.—In nine years of observation, first migrants were always seen within a 10-day period in mid-June, and peak numbers almost always occurred in the last 10 days of June (Table 1). Data for 1959 may not be accurate, as large geese were not expected, and early flocks could have been overlooked. Data from Zicus (1981) also showed that flocks leave a nesting area to molt about the same time each year, regardless of timing of the breeding season.

Numbers.—In 1969, birds passed over in flocks of 4–110 at all times of day. In late June and early July, the sun was below the horizon for 3–4 h, but there was some light at all times. We have no feeling, however, for what proportion of passage occurred at night. Flocks early in the season were often accompanied by Lesser Snow Geese (*Chen c. caerulescens*) and Tundra Swans (*Olor columbianus*).

A total of 10,292 birds was actually counted at the McConnell Delta in 1969 (Table 2), and we estimate 17,500 flew northward over the area between 07:00 and 24:00 during the entire migration period (17 June–27 July) (Fig. 1). Only 5000 birds were estimated in 1970. Despite less in-

TABLE 2
ACTUAL AND ESTIMATED NUMBERS OF LARGE CANADA GEESE PASSING THE MCCONNELL RIVER DELTA IN 1969

Date	Actual count	Additional estimated[a]	Total
17 June	28	0	28
18–19 June	0	0	0
20 June	24	0	24
21 June	5289	1724	7013
22 June	929	1700	2629
23 June	136	300	436
24 June	2176	950	3126
25 June	110	250	360
26 June	810	650	1460
27 June	245	400	645
28 June	176	350	526
29 June	90	400	490
30 June	0	0	0
1 July	2	0	2
2 July	72	200	272
3 July	0	0	0
4 July	99	150	249
5 July	—[b]	—	—
6 July	44	0	44
7 July	26	0	26
8–17 July	0	0	0
18 July	23	0	23
19–26 July	0	0	0
27 July	13	0	13
Totals	10,292	7074	17,366

[a] See Methods.
[b] No observations on this day.

tensive observations in that year, we are confident that total numbers were in fact markedly lower than in 1969. Pakulak counted 13,462 passing over Cape Churchill in 1969, but he counted only 6587 there in 1970.

Pakulak made no local counts at Churchill in the period 14–21 June 1969, as he was then engaged in extensive helicoptor surveys over a wider area. The number of migrating large Canadas seen in the wider area in that entire period came to only 2945, confirming a considerably later molt migration at Cape Churchill than at the McConnell Delta (Fig. 1).

Routes.—Birds heading NNE past the McConnell Delta (Fig. 2) were following the coastline. Many geese changed direction upon reaching the McConnell, turning away from the coastline to fly up the river (Table 3, Fig. 2). The use of landmarks by waterfowl on migration routes is common

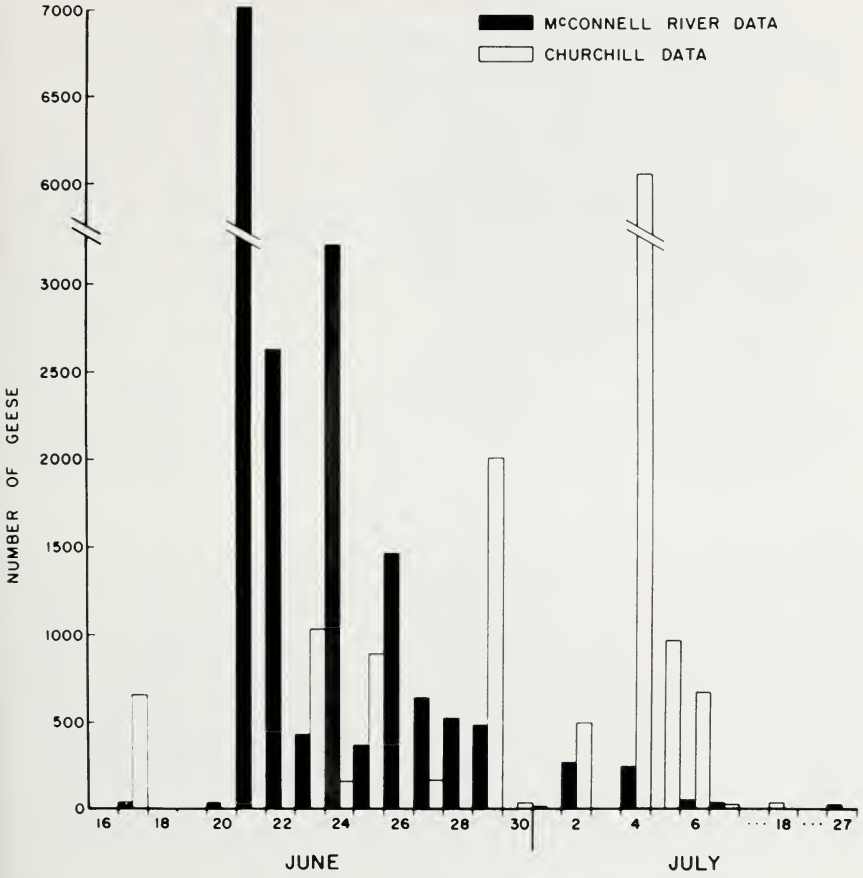

FIG. 1. Estimated daily numbers of large Canada geese flying north past the McConnell River (dark bars) and actual counts from Churchill (light bars) in 1969.

(Hochbaum 1955). Other birds heading inland at the McConnell Delta may not have changed direction, as a back-bearing for these birds is a direct line from York Factory, following the line of the coast from there to Cape Churchill. The proportions of flocks going NNE and N, NNW, or WNW were different between 1970 and each of the other 2 years (χ^2 = 68.8 and 65.3, df = 2, $P < 0.005$), but not between 1969 and 1971 (χ^2 = 2.6, df = 2, $P < 0.25$). In 1970, over 90% of the birds followed the coast NNE, while only 40% did so in the other 2 years (Table 3).

The height of migrating flocks was related to direction (Table 4), with those flocks flying highest (>150 m) tending to maintain a NNE course

FIG. 2. Position of the McConnell River with respect to known molting areas of large Canada geese (shaded). Arrows indicate main directions of molt migration past the river delta. Lengths of arrows are proportional to the numbers of geese heading in those directions in 1969 and 1971.

($\chi^2 = 35.6$, df = 2, $P < 0.005$). There was no relation between flying height and time of day of passage.

The NNW bearing from McConnell is close to being on a direct line from Cape Churchill (Fig. 2). The clear difference in timing of molt migration at the two sites (Fig. 1) indicates, however, that the birds seen at each location were not the same. Circumstantial evidence that the Churchill birds flew more directly over Hudson Bay comes from observations on 25 June 1970. A total of 5820 birds was counted leaving the Cape, but only 245 were seen at the McConnell. Ian Newton (pers. comm.),

TABLE 3

DIRECTION OF LARGE CANADA GEESE LEAVING THE MCCONNELL RIVER, NORTHWEST TERRITORIES

Flight direction[a]	Number of birds/number of flocks		
	1969	1970	1971
NNE	2679 (33)[b]/75 (31)	1480 (91)[c]/60 (92)	2003 (38)[c]/46 (33)
N	598 (7)/8 (3)		
NNW	3609 (45)/111 (46)	100 (6)/2 (3)	2475 (48)/76 (55)
WNW	894 (11)/35 (15)	15 (1)/1 (2)	663 (13)/14 (10)
Landed at McConnell	334 (4)/11 (5)	36 (2)/2 (3)	71 (1)/2 (1)
Totals	8114/240	1631/65	5212/138

[a] Birds flying NNE were flying along the coast, those flying WNW were headed upriver.
[b] Percent of column total.
[c] Combined total for NNE and N.

however, saw 591 that morning while at sea 7–12 km from shore, between the McConnell Delta and Eskimo Point (30–35 km to the north).

Origin of migrants.—Thirty-three molting large Canada geese were trapped at the McConnell River between 1960 and 1967 in banding drives of local small geese. Seven of these had been banded elsewhere. In addition, nine birds with neck bands were observed among migrating flocks. The birds with neck bands had been marked on wintering areas at Swan Lake National Wildlife Refuge in Missouri, and released there or at refuges in Arkansas and Louisiana (all in area B, Fig. 3). The birds trapped at the McConnell apparently were from the same population, as five either

TABLE 4

RELATION BETWEEN APPROXIMATE HEIGHT OF MIGRATION AND DIRECTION OF LARGE CANADA GEESE PASSING THE MCCONNELL RIVER, NORTHWEST TERRITORIES, 21–24 JUNE 1969

Flight direction[a]	Numbers of birds and flocks at heights of:		
	>150 m	30–150 m	<30 m
NNE	489 (68)[b]/11 (73)	133 (22)/7 (37)	333 (19)/8 (14)
N	232 (32)/4 (27)	0 (0)/0 (0)	77 (4)/1 (2)
NNW	0 (0)/0 (0)	416 (68)/10 (53)	992 (57)/33 (58)
WNW	0 (0)/0 (0)	61 (10)/2 (11)	344 (20)/15 (26)
Totals	721/15	610/19	1746/57

[a] Birds flying NNE were flying along the coast; those flying WNW were headed upriver.
[b] Percent of column total.

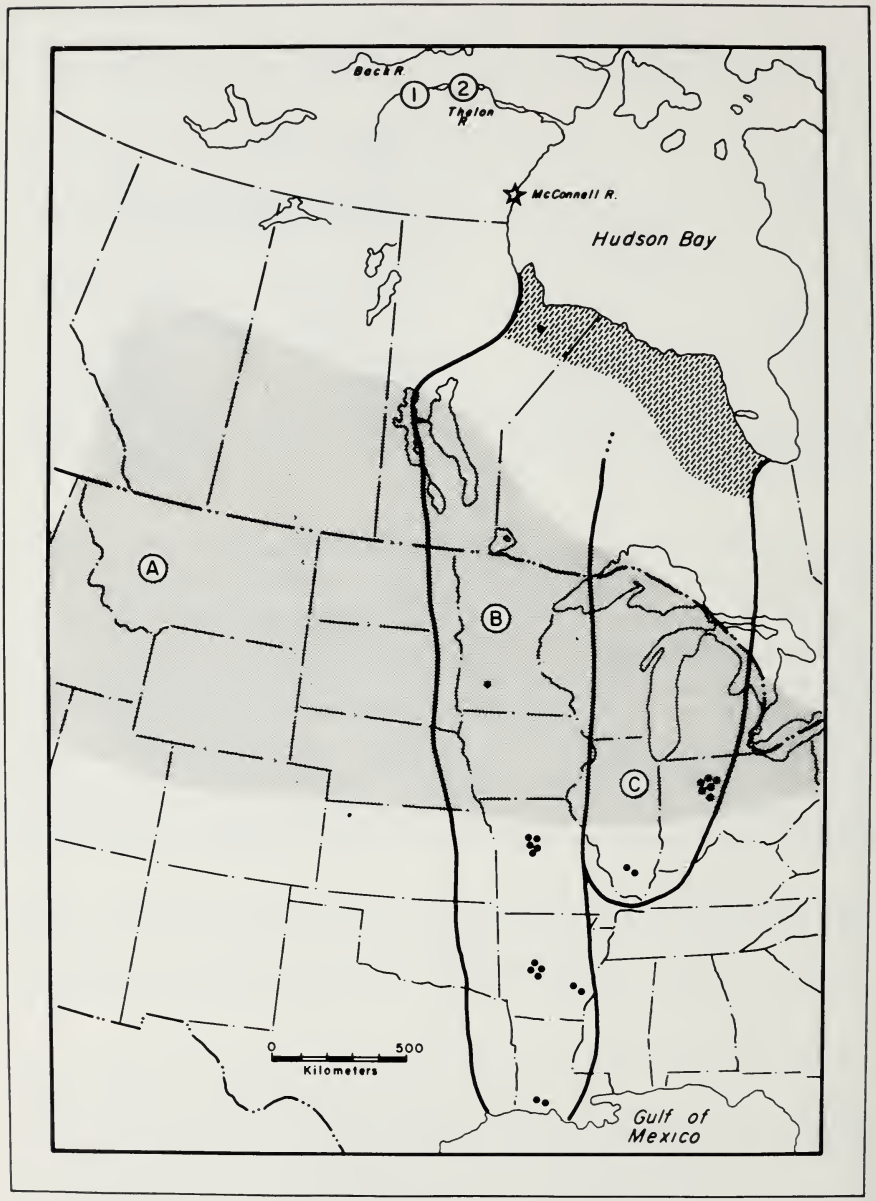

FIG. 3. Banding or recovery locations of large Canada geese seen at the McConnell river (dots). The large shaded area is the approximate breeding range of *B. c. moffitti* (including "*maxima*"), with A indicating the western part of the range. Outlined areas represent breeding (hatched) and wintering areas of *B. c. interior* in the Eastern Prairie Population

came from, or were subsequently retrapped at, those same refuges. Two birds banded at McConnell River, however, wintered in southern Illinois, one bird shot 60 km north of the McConnell River was also from Illinois, and six birds recaptured at McConnell were banded in Mercer County, Ohio (all in area C, Fig. 3). This suggests that at least three populations were involved in the McConnell River molt migration. The Ohio birds were from a known breeding population of *B. c. moffitti* (=*maxima,* Bednarik 1970). Most banded birds came from the wintering area of the Eastern Prairie Population (EPP; Vaught and Kirsch 1966) (area B, Fig. 3), with smaller numbers from the Mississippi Valley Population (MVP) (area C, Fig. 3). Two molt migrants collected at McConnell were *B. c. interior* (identified by W. E. Godfrey, National Museum of Canada, and by CDM). This is the predominant race of both the EPP and MVP wintering areas (Bellrose 1976).

DISCUSSION

Our observations suggest that at least two separate streams of large Canada geese pass by the McConnell River on northward molt migration. The first of these basically is following the Hudson Bay coast to the NNE or heading within 20°W of that.

The second major stream turns at the McConnell River and heads inland from the Hudson Bay coast on bearings well W of N, sometimes flying upriver to the NNW (Fig. 2). The first 30 km of the McConnell River has a bearing of 320°, and a direct line following that heading leads to the upper Thelon River–Lookout Point portion of a known molting area (Sterling and Dzubin 1967) (Fig. 2). A direct bearing from the McConnell to the Thelon Islands is 325–335°, close to the NNW heading of the largest number of geese we counted. Birds on these bearings fly close to the ground (Table 4).

The lack of synchrony between birds leaving Cape Churchill and those passing the McConnell River suggests that the Churchill birds constitute a third stream, perhaps passing to the east of the McConnell Delta, but we could not confirm this. The combined estimated total from narrow strips of coast at Churchill and the McConnell Delta in 1969 was 30,500, similar to the entire 30,000 estimated to be molting in the area surveyed by Sterling and Dzubin (1967). Even after we take into account any errors

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(B) and the Mississippi Valley Population (C). Numbers show sites on the Thelon River molting range where Canada geese have been trapped and banded: 1 = Lookout Point, 2 = Beverly and Aberdeen lakes (see Fig. 2).

in estimation or overlap in counts, it appears that a large fraction of west coast Hudson Bay molt migrants pass over these two points.

The geese heading NW from the McConnell appear to be heading to the central portion of the known molting area (Fig. 2), and there is circumstantial evidence in support of this being their destination. Very few molting Canadas were seen on the Thelon River in 1970 (W. Speller, pers. comm.), the same year that very few headed inland from the McConnell (Table 3). A great many molt migrants were on the Thelon in 1968 and 1969.

Kuyt (1966) and Sterling and Dzubin (1967) showed that birds molting at points 1 and 2 came mainly from areas A and B, respectively (Fig. 3). Banding data from the McConnell show that our birds are more eastern in origin and, accordingly, some may be heading farther east than the central Thelon to molt. Those birds following the coast at the McConnell could be going to currently undiscovered molting areas. Some geese still follow the coast at Eskimo Point, 35 km north of the McConnell (Pengally, pers. comm.), and small numbers have been found resting on Bibby Island, 140 km to the north (Fig. 2).

An extensive helicopter survey in 1969 of the goose habitat within 25 km of Hudson Bay between 60°N and 62°N revealed no flock of large Canada geese >110, but there were several small, widely scattered groups. Large geese following the coast north from the McConnell River may spread thinly over a wide area, making them almost impossible to count by aerial survey.

The notable regularity of molt migration timing (Zicus 1981) (Table 1), despite wide variation in the start of breeding seasons and different origins of migrants, suggests that the migration is timed to take advantage of the molting areas as soon as they become available in spring (Sterling and Dzubin 1967). On average, this would occur in late June.

The migrants themselves are primarily young birds (one to three years old, Sterling and Dzubin 1967), but unsuccessful breeding adults may also join. Changes in volume of migration may come about in two ways: when unusual reproductive success in one or two immediately preceding seasons alters the number of subadult geese, or when conditions in the current season alter the proportion of adults which do not nest successfully.

SUMMARY

Over 30,000 large Canada geese (*Branta canadensis*) pass Cape Churchill and the McConnell River delta on northward molt migration. Birds passing the McConnell are *B. c. moffitti* (sensu Palmer 1976) and *interior*, mainly from the Eastern Prairie Population, with somewhat fewer from the Mississippi Valley Population. Geese following the coastline generally fly

above 150 m, while those heading inland fly at lower altitudes. The two streams are probably going to the central Thelon River and more to the east. Birds passing Churchill migrate later and apparently pass the McConnell Delta offshore.

The time of molt migration is regular—with peak numbers in late June—but variable in volume. Breeding success the previous year probably affects numbers markedly, as most birds on molt migration are immatures.

ACKNOWLEDGMENTS

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LGL LTD., ENVIRONMENTAL RESEARCH ASSOCIATES, 22 FISHER ST., BOX 280, KING CITY, ONTARIO L0G 1K0, CANADA; MINISTRY OF NAT. RESOUR., 10 FINDLAY AVE., CARLETON PLACE, ONTARIO K0G 1J0, CANADA; AND MINISTRY OF NAT. RESOUR., WILDLIFE RESEARCH SECTION, P.O. BOX 50, MAPLE, ONTARIO L0J 1E0, CANADA. ACCEPTED 4 MAR. 1985.

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AN AERODYNAMIC BASIS FOR SELECTING TRANSMITTER LOADS IN BIRDS

Donald F. Caccamise and Robert S. Hedin

With the development of small radio transmitters, the study of animal movements under natural conditions has expanded dramatically. For most large species (>200 g), the effects of carrying a transmitter can be minimized by adjusting the size of the transmitter package. For small animals the ratio of transmitter weight to body weight is difficult to control, however, because of limitations in the size of transmitters and batteries. For flying animals aerodynamic requirements make the size of the transmitter package particularly important. An informal standard appears to have emerged for flying animals of limiting the size of the transmitter package to ≤5% of body mass. This loading is recommended widely and is adopted commonly (Cochran 1980), although the rationale for selecting 5% as the upper limit is not discussed in the literature.

Transmitters used on small birds consist of 3 basic components: (1) transmitter and antenna, (2) battery, and (3) packaging (potting material plus harness or adhesive). The weight of the transmitter and packaging can be reduced only very little, but together they generally weigh much less than the battery. Battery size can be varied; however, smaller batteries provide shorter useful field lives. In most applications involving birds, when the battery is exhausted, the radio is lost and the experiment is terminated. It is expensive (labor and capital) to equip birds with transmitters, and there are scientific benefits in maximizing the length of the observation period on individual subjects.

Another important concern is the effect of the transmitter on overall energy balance and behavior of the subject. Energetic costs of powered locomotion increase with additional weight, and in flight the increase can be substantial. Increases in energy demand are likely to influence behavior. Estimates of the added transportation costs of transmitters can be helpful in selecting transmitters of appropriate size and may also aid in interpreting behavioral responses of experimental subjects. A method is needed to select transmitter size according to both the flying ability of experimental subjects and the energetic cost of transport. Such an approach would greatly increase the efficiency of telemetry studies on birds.

For reasons we will explain below, transmitter weights based on a fixed percentage of body weight (e.g., 5%) affect flight characteristics of large birds more than those of small birds (Tucker 1977). Also, use of a fixed percentage of body weight provides no easy method of estimating the

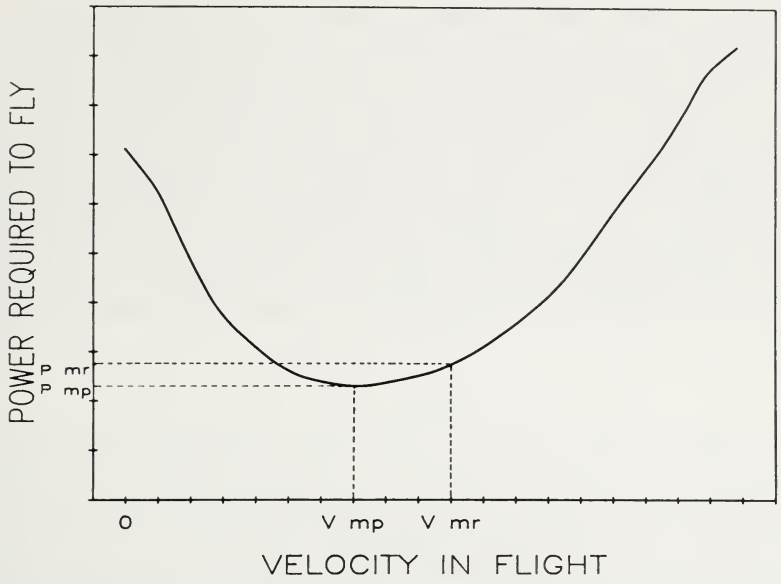

FIG. 1. The solid line represents the generalized relationship between flight velocity and power requirements for flight. The upper and right broken lines illustrate the relationship between V_{mr} and P_{mr}. V_{mp} is the velocity requiring the minimum amount of power (P_{mp}) necessary to fly in level flight (after Pennycuick 1969).

energetic cost of transporting the transmitter. We have developed a method to select transmitter weights based on flight characteristics. As the method is based on power requirements for flight, estimates of the added cost of transportation due to the transmitter can be made. We provide a general method based solely on body mass and indicate how estimates can be refined for individual species by taking simple measurements of wing morphology and wing beat frequencies.

BIRD FLIGHT

The power required for a bird to fly varies with flight velocity. At very low velocities (e.g., hovering) power requirements are very high, at intermediate velocities power requirements are low, and at high velocities power requirements are again high (Fig. 1). Within the range of intermediate velocities for any species, there is a particular velocity at which the bird can fly most efficiently; that is, it can travel the greatest distance per unit of energy expended (Pennycuick 1969). This is termed the velocity of maximum range (V_{mr}) (Appendix 1). Power required to fly at V_{mr} is P_{mr}.

In flight a bird is able to produce power at some maximum rate, but the maximum rate can be sustained for only brief periods as the bird quickly tires. Power output, however, can be sustained for extended periods at lower rates of power production. The maximum sustainable rate of power production is termed available power (P_a). P_a can be calculated as the product of flight muscle mass, wing beat frequency, and specific work of flight muscles (Appendix 2, Pennycuick 1969). In general P_a is greater than P_{mr}, and the difference between these values can be used to indicate the amount of surplus power (P_s) the bird has available. A portion of P_s is used whenever a bird transports the additional weight of a transmitter.

CALCULATIONS

To estimate power requirements for flight, we used methods discussed in Pennycuick (1969) and Tucker (1973). Specific equations and methods are detailed in Appendixes 2 and 3, where we also provide instructions on how to obtain a computer program to perform the calculations. As each variable in the equations can be resolved to a function of body mass, we performed our calculations using these allometric relationships. Such relationships reduce the variation among a large number of individuals to a single value. Therefore, the results of our calculations using allometric relationships represent estimates for dimensionally "average birds." These are useful for demonstrating general relationships, but estimates for any specific species can be greatly improved by taking several simple measurements (Appendix 3).

Body mass of small birds generally shows considerable diurnal and seasonal variation resulting primarily from changes in fat accumulation. In our calculations we wanted to be sure of developing conservative estimates for flight abilities in order to minimize the chance of overloading any bird. We began by defining base mass (m_b) as a minimum level representing birds having empty stomachs and little fat. For a given species, certain characteristics such as wing size, mass of flight muscle, and wing beat frequency remain relatively constant irrespective of changes in body mass. Calculations for these values were based on m_b (Appendix 2).

For small birds, changes in body mass due to fat accumulation can exceed 50% of m_b (e.g., Odum et al. 1961). Adjusting m_b to reflect possible increases in fat accumulation assures conservative estimates of flight abilities. We calculated an adjusted body mass by increasing m_b by 50%. The adjusted mass ($m_a = 1.5m_b$) was used in all calculations except those involving morphological relationships (see above and Appendix 3). In working with individual species, size of the adjustment can be changed

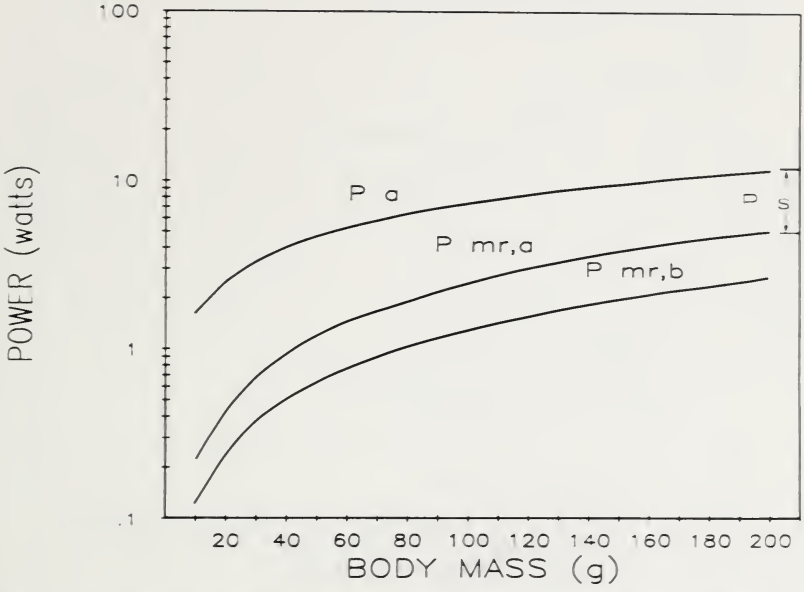

FIG. 2. The top line represents the total power available (P_a) for flight in relation to body mass. The bottom 2 lines are the power required to fly at V_{mr} for birds at base mass ($P_{mr,b}$) and adjusted mass ($P_{mr,a}$). Each relationship increases with mass, but $P_{mr,b}$ and $P_{mr,a}$ increase more rapidly. Thus, P_a and $P_{mr,b}$ converge at about 4645 g. S = surplus power.

to reflect the expected range of variation in m_b that would normally occur during the experiment.

Because power requirements vary with flight velocity, it was necessary to select a single velocity on which to base calculations. Hovering flight and flight at very slow speeds are based on unique aerodynamic relationships, so we excluded these from consideration (Pennycuick 1969). It has been suggested (Schnell and Hellack 1979) that birds most often fly at or below their most efficient speed. We, therefore, selected V_{mr} as the basis for all calculations.

In flight a bird produces drag in proportion to the size of its frontal area. Attachment of a transmitter increases drag by increasing frontal area. We included a function in the model to account for increased frontal area resulting from the transmitter (Appendix 2, equation 6). The effect increases with transmitter mass. This again provides for conservative estimates of flight capabilities.

RATIONALE

Larger birds are able to produce more power than smaller ones, so P_a is an increasing function with body mass (Fig. 2). Similarly, power re-

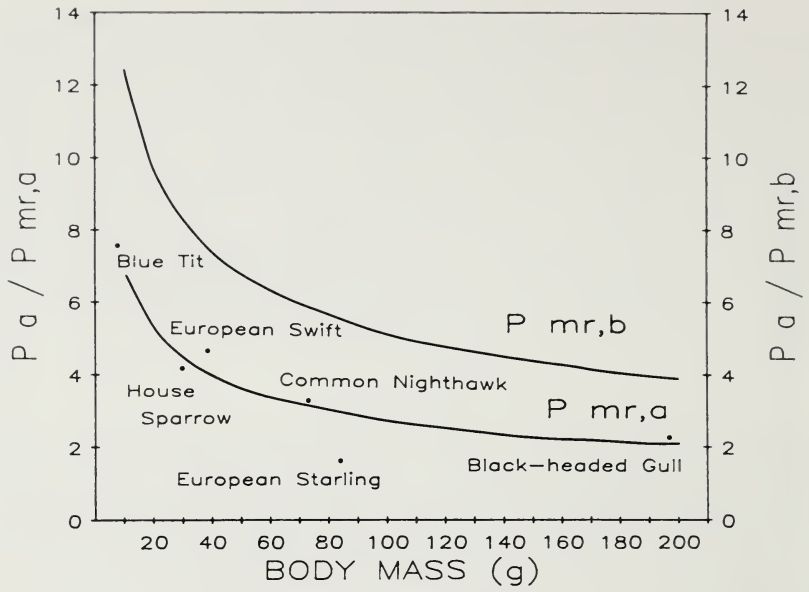

FIG. 3. The ratio of surplus power (P_s) to power required to fly at V_{mr} ($P_{mr,a}$). The upper line represents birds at base mass (m_b) and the lower line adjusted mass (m_a). This ratio provides a relative measure of the amount of surplus power available according to body mass and illustrates that small birds can carry much larger loads relative to their body mass than large birds. Measurements for the illustrated species come from Caccamise 1974 (Common Nighthawk, *Chordeiles minor*) and Greenewalt 1962 (Blue tit, *Parus caeruleus*; European Swift, *Apus apus*; House Sparrow, *Passer domesticus*; European Starling, *Sturnus vulgaris*; Black-headed Gull, *Larus ridibundus*).

quired to fly at the most efficient speed ($P_{mr,b}$), while lower than P_a, also increases with body size. The power curve using adjusted mass ($P_{mr,a}$) is identical to that using m_b, except it is elevated. This indicates increased power requirements when a bird is heavier (Fig. 2). In our calculations, the difference between amount of power needed to fly at V_{mr} ($P_{mr,a}$) and amount of power available (P_a) is termed surplus power (P_s). It is represented by the magnitude of the difference between the two curves (Fig. 2).

As $P_{mr,b}$ increases faster than P_a, these are convergent functions, and they eventually meet. This point represents the largest dimensionally average bird that can fly continuously at V_{mr}. Our estimates indicate that this would happen at a base mass of 4645 g. A dimensionally average bird of this size would have no surplus power when traveling at V_{mr} (i.e., $P_s = 0$). It would not be able to carry any additional weight without producing power at rates greater than P_a. While power could be produced for short intervals at such rates, sustained powered flight would not be

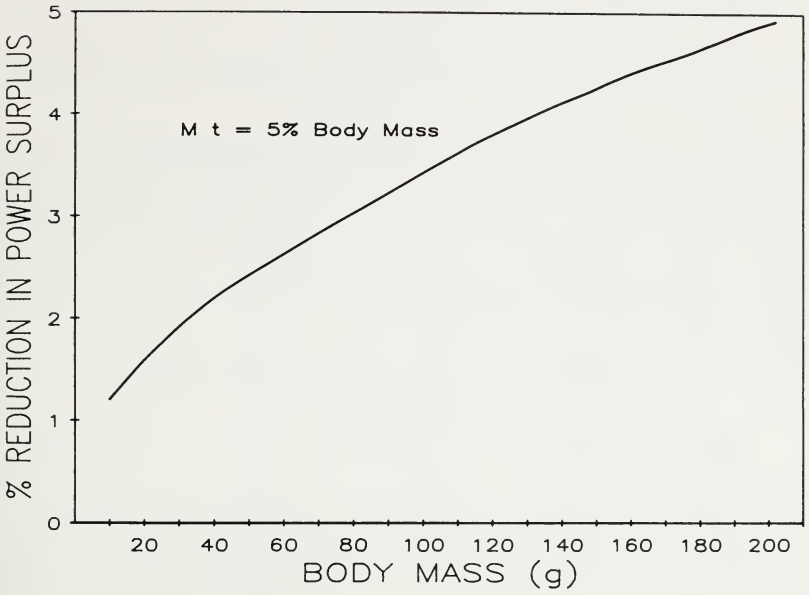

FIG. 4. Percent reduction in P_s according to body size (m_b) when transmitter is 5% of body mass. Selection of transmitter size using a single percentage of body size results in relatively greater reductions in power surplus for large birds than for small birds.

possible at velocities as high as V_{mr}. By comparison, P_a for small birds is much greater than $P_{mr,b}$, so surplus power is relatively large (Fig. 2).

The relative difference in P_s between large and small birds is the result of scaling effects. For example, differences in mass between large and small birds are relatively greater than differences in external dimensions. This is illustrated by the relationship between wing span and mass (Appendix 2, equation 4) where wing span increases with mass to the 0.33 power.

The ratio of $P_a/P_{mr,a}$ provides a means to evaluate the relative magnitude of P_s (Fig. 3). For example, species in the 20–30 g range can produce sufficient power to transport loads several times their body mass and still remain below P_a. As body mass increases, the power ratio declines until P_a and $P_{mr,b}$ are equal (body mass = 4645 g) when the power ratio equals 1 and power surplus equals 0.

P_a is determined using morphological characteristics, so it is constant for an individual bird with fixed dimensions or for a species if we use average dimensions. The effect of adding a load in the form of a transmitter is to increase the amount of power required to fly at a given speed (including V_{mr}). The additional power requirements reduce P_s because $P_{mr,a}$

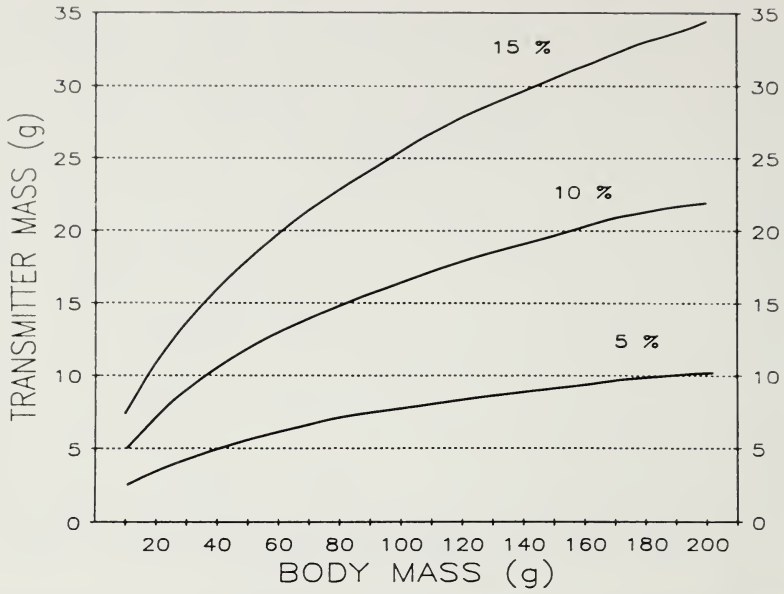

FIG. 5. The 3 lines represent the relationship between body mass (g) and transmitter mass (g) resulting in 5%, 10%, and 15% reductions in power surplus. These relationships can be used to select transmitter size according to the predicted decrease in power surplus caused by the added load. While these values represent good estimates for "average" birds, estimates can be improved for individual species by calculating values based on several simple measurements of wing morphology and flight characteristics (Appendix 3).

is elevated to a new higher level. As power required for flight is proportional to mass, adding to body mass by a fixed proportion will increase power requirements the same relative amount irrespective of body size. Therefore adding a transmitter weighing a fixed percentage of body mass increases power requirements the same proportionate amount for any sized bird (ignoring the slight effect of added transmitter drag). For example, equipping a 50-g bird with a 2.5-g (5% of body mass) transmitter will increase $P_{mr,a}$ by 7.7%. Likewise a 10-g transmitter on a 200-g bird will also increase $P_{mr,a}$ by about 7.7%.

A bird's ability to carry additional weight is determined by the resulting proportionate decline in P_s. Because P_s decreases with increasing body mass, adding a load as a fixed percentage of body mass reduces P_s relatively more for large birds than for smaller ones (Fig. 4). This results in relatively conservative loadings for small birds and liberal loadings for large birds. The use of a fixed percentage of body mass, therefore, does not result in a uniform effect over a range of body sizes.

For a bird of any given mass, it is possible to determine the transmitter

TABLE 1

FLIGHT PARAMETERS OBTAINED BY MEASUREMENT AND ALLOMETRY FOR THE EUROPEAN STARLING

Symbols	Allometric determination		Measurement (in part)[a]		Units	Equation or source[b]
	Base mass	Adjusted mass	Base mass	Adjusted mass		
m_b	0.0845	—	0.0845	—	kg	G
m_a	—	0.1267	—	0.1267	kg	—
m_f	0.0144	0.0144	0.0185	0.0185	kg	2, G
m_t	8.45×10^{-3}	8.45×10^{-3}	8.45×10^{-3}	8.45×10^{-3}	kg	—
b	0.4827	0.4827	0.3745	0.3745	m	4, G
f	8.07	8.07	5.10	5.10	no./sec	5, G
A	6.54×10^{-4}	8.54×10^{-4}	6.54×10^{-4}	8.54×10^{-4}	m^2	3, T
S_d	0.1829	0.1829	0.1101	0.1101	m^2	8
V_{mr}	10.48	12.00	11.89	13.63	m/sec	9
P_a	6.61	6.61	5.38	5.38	watts	7
$P_{mr,b\|a}$	1.21	2.24	1.72	3.19	watts	13
P_s	5.40	4.36	3.65	2.17	watts	14
P_s'	—	4.04	—	1.72	watts	14
$P_{mr,a}'$	—	2.57	—	3.66	watts	13
R_p		5.9		12.4	%	15

[a] Measurements from the literature were used where available, otherwise parameters were determined allometrically as indicated.

[b] Allometric equations are referred to by numbers corresponding to equations in Appendix 2. Literature sources are referred to by letters: G = Greenewalt 1962, T = Tucker 1973.

mass that will result in any particular reduction in P_s. We performed this process over a series of body sizes and for reductions in power surplus of 5, 10, and 15% (Fig. 5). The curves increase rapidly over the smaller body sizes but quickly level off. This results from the relatively large P_s of small birds as opposed to large ones. Thus, for a given reduction in surplus power, a small bird can carry a greater proportion of its body weight than a large bird. For example, allowing a 15% reduction in P_s, a 20-g bird can carry a transmitter weighing over 50% of its body mass, while a 200-g bird can carry only 8% (Fig. 5).

Fig. 5 can be used to estimate the relative cost of transporting a transmitter by any bird weighing less than 200 g. The initial step is to decide the amount of reduction in surplus power that is appropriate for the particular experiment. As an initial guideline, the values represented in Fig. 4 indicate levels of reduction that result from the generally accepted loading of 5% of body mass. For example, an 80-g European Starling (*Sturnus vulgaris*) carrying a 4-g transmitter (5% of m_b) (Fig. 4) would give up only about 3.2% of its surplus power. Starlings are able to carry much heavier loads with no apparent effect on travel between foraging and roosting sites, as we have had them carry transmitters equal to about

8% of m_b (m_b = 80 g, m_t package = 6.5 g) for as long as 133 days (Caccamise et al. 1983). If it is decided that a 5% reduction in P_s is acceptable, then in Fig. 5 at a body mass of 80 g, the 5% line corresponds to a transmitter mass of 6.8 g.

These values are only approximations, as the relationships shown were determined allometrically for average-size birds. Values that better represent individual species can be calculated using equations provided in Appendix 2. Accuracy of the generalized relationships for individual species depends on how closely the flight characteristics of each particular species approach average values. In Fig. 3, the points represent values calculated from actual measurements of birds obtained from the literature, while the lines were determined entirely from allometric equations. Some species were quite close to predicted values while others were not.

In Table 1 we compare pertinent flight parameters for the European Starling obtained by measurement and allometry. In Fig. 3 the starling is not close to the line representing "average" birds. Therefore, this species illustrates the process of calculation as well as sources of variation between measured and allometric values. The greatest differences are in overestimates of wing span and flapping rate by the allometric equations. The overall result is that P_a is lower and $P_{mr,b, \text{ and } a}$ are higher. This leads to an underestimate of the transmitter effects by the allometric equations.

CONCLUSIONS

The aerodynamics of bird flight are certainly too complicated to be interpreted in terms of a single measure like P_s. There are yet many factors that are only poorly understood. For instance, the large P_s of small birds indicates that they can carry several times their body weight while maintaining $P_{mr,a'}$ below P_a, but there is no way to predict the importance of such a large surplus in their normal activities. A large P_s probably contributes to specialized skills such as take-offs, landings, and general maneuverability. Also, how and where the transmitter is attached are important, as changes in the center of gravity will affect flight characteristics. Although P_s does provide a method to estimate a bird's ability to transport additional weight, its relationship to other aspects of flight awaits further research. Notwithstanding its shortcomings, this method seems to be a suitable approach for estimating the impact of a transmitter on power requirements for flight, and is likely to provide a better basis for determining transmitter size than methods used in the past.

SUMMARY

An accepted practice in radio telemetry studies is to limit transmitter size to 5% of body mass irrespective of bird size. This approach is unsatisfactory because it (1) ignores aero-

dynamic relationships indicating that small birds can carry loads equaling a larger proportion of their body mass than large birds, and (2) fails to provide an estimate of energetic costs of transporting the transmitter. We developed a method to select transmitter mass based on estimates of power requirements for flight and total power available for flight. We provide a general method based only on body mass, but we also show how estimates can be improved for individual species by taking several simple measurements.

A minimum value for body mass is selected considering factors affecting weight such as annual cycle. This is the base mass and is used to calculate the maximum sustainable rate of flight power (power available). Next, power requirements for flight are calculated. As power requirements vary with flight velocity, a single velocity must be selected: we use the most efficient velocity. To assure conservative estimates of a bird's ability to carry a transmitter, base mass is adjusted upwards by a percentage approximating the normal range in body mass. Adjusted mass is used to estimate the power required to fly at the most efficient velocity. The difference between power available for flight and the power required to fly at the most efficient velocity is surplus power. Adding a transmitter increases power requirements. We evaluate a bird's ability to carry a transmitter by calculating the reduction in surplus power caused by transmitters of various sizes.

Power surplus is proportionately greater for small birds than large birds, so basing transmitter size on a fixed percentage of body mass results in conservative loadings for small birds and liberal loadings for large birds. Our method allows an investigator to select transmitter size according to the reduction in power surplus that is considered appropriate for the experimental conditions, and at the same time it provides an estimate of the energetic cost of transporting the added mass of the transmitter.

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Appendix 1

Symbols and Constants Used in Calculations

Symbol	Definitions and units
′	Indicates that transmitter effect has been included in the calculation.
A	Equivalent flat-plate area—the area of a flat plate yielding a drag equivalent to that produced by the frontal area of the bird (m^2).
A′	Equivalent flat-plate area of the bird plus that of the transmitter (m^2).
A_t	Equivalent flat-plate area of the transmitter (m^2).
b	Wing span from tip of one wing to tip of other (m).
f	Flapping frequency (no./sec).
m_a	Adjusted mass of bird—in our examples this equals base mass plus 50% (kg). The value can be changed to reflect range in body mass expected for any given species.
m_a'	Adjusted mass of bird plus mass of transmitter (kg).
m_b	Base mass of bird assuming minimum fat reserves, empty crop and stomach, and no transmitter (kg).
m_f	Mass of flight muscles (kg).
m_t	Mass of transmitter (kg).
p	Air density at sea level (1.18 kg/m^3). We used sea level for our calculations but this should be changed to reflect the elevation where the bird will be carrying the transmitter.
P_a	Available power (watts)—maximum sustainable rate of power output in flight.
P_i	Induced power (watts)—power needed to overcome force of gravity.
$P_{mr,a}$	Power maximum range (watts)—power required to fly at the most efficient velocity (greatest distance per unit of energy consumed) for birds at adjusted mass.
P_o	Profile power (watts)—power required to overcome profile drag of the wing as it moves through the air.
P_p	Parasite power (watts)—power required to overcome resistance of the body moving through air.
P_s	Surplus power (watts)—the difference between amount of power required to fly at V_{mr} ($P_{mr,a}$) and total amount of power available (P_a).
R_p	Proportionate reduction in surplus power caused by added costs of transporting a transmitter.
Q	Specific work of flight muscles (57 joules/kg).
S_d	Wing disk area—the circular area through which the flapping wings travel (m^2).
V_{mr}	Velocity maximum range (m/sec).

Appendix 2
Equations Used in Calculations

Number	Equation	Explanation (source)
1	$W = mg$	Where m equals any mass (kg) and g is acceleration of gravity (9.81 m/sec^2).
2	$m_f = 0.17m_b$	(Pennycuick 1969)
3	$A = 0.00334m_a^{0.660}$	(Tucker 1973)
4	$b = 1.1m_b^{0.3333}$	(Tucker 1973)
5	$f = 3.816/b^{1.029}$	(derived using data in Greenewalt 1962)
6	$A_t = 0.00334m_t^{0.660}$	Flat-plate area where m_t is in kg (Tucker 1973)
7	$P_a = m_f Qf$	(Pennycuick 1969)
8	$S_d = 0.785b^2$	(Tucker 1973)
9	$V_{mr} = 1.13\left(\frac{(9.81m)^{0.5}}{p^{0.5}A^{0.25}S_d^{0.25}}\right)$	(Pennycuick 1973)
10	$P_i = \frac{2(9.81m)^2}{3.14159pb^2RV_{mr}}$	where R = 0.7 (Tucker 1973)
11	$P_p = \frac{pAV^3}{2}$	(Tucker 1973)
12	$P_o = 1.8m_a^{-0.16667}V_{mr}^{-0.5}(P_i + P_p)$	(Tucker 1973)
13	$P_{mr,a} = P_i + P_p + P_o$	(Tucker 1973)
14	$P_s = P_a - P_{mr,a}$	
15	$R_p = \frac{P_{mr,a}' - P_{mr,a}}{P_s}$	

Appendix 3

Methods Used to Perform Calculations for Individual Species[a]

1. Determine m_b, remembering to consider age, stage of the annual cycle (e.g., premigratory), and other factors that might affect weight of the bird. This should represent a minimum normal mass. Then calculate m_a using an adjustment (% m_b) reflecting the expected range in body mass that would normally occur during the study. In our examples we used 50%.
2. Determine mass of flight muscles (m_f), wingspan (b), and flap frequency (f). This is best accomplished by direct measurement of individual species, but allometric equations (2, 4, and 5 respectively) can be used. Mass should be m_b.
3. Calculate P_a (equation 7).
4. Determine appropriate air density (ρ) for elevation where your experimental subjects will live, and then calculate the following: A, S_d, and V_{mr} (equations 3, 8, and 9). Mass should be m_a both here and in step 5.
5. Using equations 10–12, calculate P_i, P_p, and P_o; then combining these in equation 13, calculate $P_{mr,a}$.
6. Surplus power can now be calculated (equation 12).
7. Determine the mass, and calculate (equation 6) the equivalent flat-plate area of the transmitter. Calculate A′ as $(A + A_t)$.
8. Calculate m_a' by adding the mass of the transmitter to m_a.
9. Using A′ and m_a' repeat steps 4–5 to calculate the same values, but including the effects of the transmitter.
10. Using equation 13, calculate the proportional reduction in surplus power caused by the transmitter (equation 15).

[a] A computer program that will perform all necessary calculations is available from the first author. To obtain a copy of the program, send a formatted (IBM-PC compatible, DOS 2.0), 5.25 in. floppy disk to Donald F. Caccamise, Dept. Entomology and Economic Zoology, Rutgers University, New Brunswick, New Jersey 08903.

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NEST SITE USE BY CAVITY-NESTING BIRDS OF THE CARIBOO PARKLAND, BRITISH COLUMBIA

Barbara Peterson and Gilles Gauthier

Several birds and mammals build their nests in cavities located in the trunks or large branches of dead or dying trees. Many of these species are secondary cavity nesters and use natural cavities formed by decay or, more commonly, excavated by primary cavity nesters such as woodpeckers (Zeleny 1977). Cavity-nesting is advantageous because cavities protect the brooding female and the offspring from weather and predators (von Haartman 1957, Zeleny 1977). Consequently, breeding success of cavity nesters is generally much higher than that of other birds.

One drawback of cavity nesting is that inter- and intraspecific competition for nest sites may be severe. Several lines of evidence show that natural cavities are often limited: (1) addition of nest boxes has resulted in large increases in populations of some hole nesters (von Haartman 1957, Strange et al. 1971, Hamerstrom et al. 1973); (2) all suitable cavities are sometimes used by cavity nesters (van Balen et al. 1982); and (3) interspecific competition has been observed in the form of fights between nesting birds or destruction of nests by competitors (von Haartman 1957; Erskine 1959, 1964, pers. obs.).

The availability of suitable nest sites may therefore be critical in determining population numbers and community composition among secondary cavity nesters. Snyder (1977) proposed three levels of limitation for these cavity nesters. First, there may be an intrinsic scarcity of adequate nest sites relative to other necessary resources. Second, the suitability of a nest site might be constrained by its vulnerability to competitors and predators. Third, there may be behavioral limitations in the abilities of species to locate existing nest sites.

The interior of British Columbia has a rich cavity-nesting community (McLaren 1963). In the early fifties, the European Starling (*Sturnus vulgaris*) invaded the area, and Erskine and McLaren (1976) predicted that competition for nest sites would increase as a result of this change in the avian community. The objectives of this study were to (1) characterize differences in nest sites among six cavity-nesting species, (2) compare nest site characteristics found in this study with similar data collected by McLaren (1963) 24 years ago, and (3) assess the degree of competition for nest sites in this community in relation to presence of starlings.

METHODS

The study was conducted 15 km north of 100 Mile House in the Cariboo Parkland region of British Columbia. The study area covers about 20 km² of rolling grassland, small groves of aspen (*Populus tremuloides*), and boreal forest of Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*). Although boreal forest is dominant in the general area, about ⅔ of the study area was located in the parkland habitat. The study area included eighteen ponds and two lakes ranging in size from <1 ha to 60 ha.

Cavities were located by intensive searches of all suitable trees. Most of the searching effort was concentrated on trees within 200 m of the ponds and lakes from the first week of May to the beginning of July 1983. Overall, about 250 ha were searched thoroughly for cavities. Each cavity was mapped, marked with flagging tape, and revisited at least twice to determine if the cavity was being used, and by what species. Cavities were reached using ladders or spurs, and they were inspected with a periscope (De Weese et al. 1975). A cavity was labeled as empty if no eggs or fresh nesting material had been detected by the end of July.

McLaren (1963) divided the hole-nesting community of the Cariboo in three cycles according to the size of the cavity and its primary cavity nester: the small cavity cycle of the Yellow-bellied Sapsucker (*Sphyrapicus varius*), the midsize one of the Northern Flicker (*Colaptes auratus*), and the large one of the Pileated Woodpecker (*Dryocopus pileatus*). Our study concentrated on cavities of the "flicker cycle," which are the most abundant in the area. Species using flicker cavities form a discrete community except for the Tree Swallow (*Tachycineta bicolor*), which readily uses both sapsucker and flicker cavities (McLaren 1963). Thus, species included in this study used only flicker cavities (>4.5 cm in entrance diameter), except for the swallows, which used cavities >3.5 cm in entrance diameter.

All nest sites where the resident species was known were measured, except for cavities occupied by starlings and swallows, where we randomly selected 43 and 31 cavities, respectively, for measurement. A few cavities were used by two species at different times during the breeding season. In such cases, we included that cavity's measurements twice (once for each species) in the analysis. Measurements were made near the end of July after young had fledged from the nests.

Nineteen variables were measured at each nest site. Habitat variables included: the dominant tree species, an index of tree density in the grove, and the height of the understory vegetation. The basal area was used as an index of tree density. Basal area was measured one m in front of the tree using a forester prism (basal area factor of 6 m²/ha/tree).

The six variables describing the nesting tree included: the diameter at breast height, the height of the nesting tree, the canopy height from the ground to the bottom of the crown canopy, the distance to water (pond or lake), the distance to the nearest obstruction in front of the cavity entrance, and the distance to the nearest edge of the stand of trees. Canopy height was measured using a surveyor level, and snags in open areas were assigned a value of 20 m, the highest canopy measured in this study. We also noted the tree species and whether the tree was dead or alive.

Ten cavity variables included: the horizontal and vertical diameter of the entrance, the compass direction that it faced, the height of the entrance above the ground, the depth of the cavity from the bottom edge of the entrance to the floor, the breadth from the inside edge of the entance to the back wall, and the width between the two side walls at the entrance level. Width and breadth were measured using a collapsing ruler; depth was measured using a plumb bob. We used these inner dimensions to calculate the volume of the cavity (depth × breadth × width), the floor area ($\pi \times$ ½ breadth × ½ width), and the area of the cavity entrance ($\pi \times$ ½ vertical × ½ horizontal diameter). In addition, we noted the type of nesting material, if any, within the cavity.

A few variables were not normally distributed, and these were transformed by $\log(x + 1)$ to allow the use of parametric statistics (Sokal and Rohlf 1969:384). We first performed a one-way analysis of variance (ANOVA) on each variable to test for differences among species.

A discriminant function analysis (DFA) was then performed to characterize the type of cavity used by each species. Only variables that were statistically significant (using the criterion $P < 0.1$) in the ANOVA were included in the DFA. This procedure reduces the number of variables in the DFA and eliminates variables that contribute little a priori to separation among groups (Pimentel 1979, Mackenzie and Sealy 1981). Correlations among cavity measurements were checked to ensure that they were not highly dependent.

The DFA uses the observed variables to produce a linear function that maximizes separation among species by maximizing among-group to within-group sums of squares (Jeffers 1978, Williams 1983). The accuracy of the discriminant function model was evaluated using the Jackknife procedure (Jeffers 1978, Williams 1983, Willner et al. 1983). This method makes efficient use of cases, as one case is omitted each time a discriminant function is computed. This model is then used to classify independently the excluded cases. Statistical analyses were performed with the MDA computer program.

RESULTS

Of the 311 cavities found, 176 (57%) were occupied at some time during the breeding season. Nine different species used these cavities: starling (44%), Tree Swallow (19%), Bufflehead (*Bucephala albeola*) (15%), Northern Flicker (8%), Mountain Bluebird (*Sialia currucoides*) (4%), flying squirrel (*Glaucomys sabrinus*) (3%), American Kestrel (*Falco sparverius*) (2%), Northern Saw-whet Owl (*Aegolius acadicus*) (2%), and red squirrel (*Tamiasciurus hudsonicus*) (2%). Kestrels, owls, and red squirrels were deleted from the following analysis because of small sample sizes ($N < 5$).

Unlike cavity excavators, most secondary cavity nesters line their nest with vegetation or feathers (pers. obs.). Among the 135 unoccupied cavities, only 6 contained no nesting material and therefore showed no sign of previous use by any secondary cavity nesters. We did not determine, however, the proportion of unused cavities that were still suitable. Eighty-three percent of the used cavities were in aspens and 47% were in dead trees.

Univariate analysis.—Eighteen variables were tested using ANOVA to see if they varied significantly among the 6 species (dominant tree species was excluded since it is a discrete variable). The results (Table 1) showed that the following 6 variables were not significant ($P > 0.1$): tree density, height of understory, height of nesting tree, distance to water, compass direction of the entrance, and height of the entrance. These variables were eliminated. The cavity variables differed much more among species than did the habitat or nest tree variables (Table 1). Entrance diameter and inner cavity dimensions were also deleted from the remaining analysis as these variables were highly correlated with entrance area and cavity volume.

TABLE 1

RESULTS OF ONE-WAY ANALYSIS OF VARIANCE FOR 18 VARIABLES CHARACTERIZING NEST SITES OF 6 SPECIES OF CAVITY NESTERS IN THE CARIBOO PARKLAND, BRITISH COLUMBIA[a]

Variables	*F* values	*P*
Habitat variables		
Tree density	1.808	0.12
Height of understory	1.572	0.14
Tree variables		
DBH of nesting tree	2.282	0.051
Height of nesting tree	0.438	0.90
Canopy height	5.746	<0.001
Nearest water	1.210	0.31
Nearest entrance obstruction	1.914	0.097
Nearest edge of stand	2.278	0.052
Cavity variables		
Compass direction	1.082	0.37
Height of cavity entrance	0.631	0.67
Cavity volume	25.402	<0.001
Entrance area	5.937	<0.001
Floor area	15.511	<0.001
Vertical entrance diameter	2.869	0.018
Horizontal entrance diameter	4.694	<0.001
Width of cavity	15.594	<0.001
Breadth of cavity	8.495	<0.001
Depth of cavity	8.300	<0.001

[a] See Table 2 for sample sizes.

Swallows and bluebirds were found to occupy the smallest cavities, flickers and Buffleheads occupied the largest ones, and starlings and squirrels occupied intermediate sized cavities (Table 2). Nest sites of flickers, Buffleheads, and bluebirds were characterized by having few obstructions in front of the cavity entrance. Bluebirds tended to nest in open habitat, flickers and Buffleheads in sparsely treed groves, starlings on the edges of dense stands, and squirrels within denser forests (Table 2).

Multivariate analysis.—Species with small sample size ($N < 14$) were excluded from the DFA, as suggested by Williams (1983). The analysis thus included only starlings, swallows, Buffleheads, and flickers. The test for homoscedasticity showed that the variance-covariance matrices were homogeneous (Box's $M = 85.2$, $F = 1.187$, $df = 63,9743$, $P > 0.1$).

Three discriminant functions were derived from the analysis, although only the first two were significant (χ^2 test, $P < 0.05$) (Table 3). These two factors accounted for 97.2% of the discriminating power of the model.

TABLE 2

CHARACTERISTICS OF NEST SITES FOR 6 CAVITY-NESTING SPECIES OF THE CARIBOO PARKLAND, BRITISH COLUMBIA

	Bufflehead	Northern Flicker	European Starling	Mountain Bluebird	Tree Swallow	Flying squirrel
N	26	14	41	7	31	6
Tree density (m^2BA^a/ha)	27 ± 3[b]	21 ± 4	35 ± 4	22 ± 9	33 ± 4	40 ± 7
DBH (cm)	33.0 ± 1.4	30.0 ± 2.0	31.1 ± 1.1	29.1 ± 1.8	27.3 ± 0.9	30.4 ± 2.9
Canopy height (m)	9.1 ± 1.5	16.5 ± 1.6	5.9 ± 0.7	6.4 ± 2.4	9.1 ± 1.2	9.0 ± 2.4
Nearest entrance obstruction (m)	7.7 ± 0.7	9.1 ± 0.6	7.1 ± 0.6	10.0 ± 0.1	6.6 ± 0.7	5.9 ± 1.9
Nearest edge of stand (m)	5.0 ± 1.1	5.1 ± 1.6	2.2 ± 0.5	0.4 ± 0.4	3.5 ± 1.1	4.7 ± 2.1
Vertical entrance diameter (cm)	7.4 ± 0.5	7.5 ± 0.3	6.9 ± 0.4	7.0 ± 1.1	5.5 ± 0.4	5.9 ± 0.4
Horizontal entrance diameter (cm)	6.8 ± 0.1	6.9 ± 0.5	6.3 ± 0.2	5.8 ± 0.7	5.2 ± 0.3	6.1 ± 0.3
Width of cavity (cm)	14.0 ± 0.4	13.3 ± 0.6	12.4 ± 0.4	9.7 ± 1.3	8.9 ± 0.4	11.8 ± 0.5
Breadth of cavity (cm)	15.7 ± 0.6	14.9 ± 0.6	15.0 ± 0.5	12.7 ± 0.9	11.6 ± 0.4	13.0 ± 1.1
Depth of cavity (cm)	35.3 ± 3.0	33.7 ± 2.5	26.4 ± 1.7	19.9 ± 5.1	17.5 ± 1.7	26.7 ± 2.1
Volume of cavity (cm^3)	6212 ± 698	5251 ± 537	3831 ± 303	2362 ± 990	1534 ± 249	3149 ± 229
Floor area (cm^2)	175 ± 10	158 ± 12	149 ± 8	97 ± 15	82 ± 5	123 ± 15
Entrance area (cm^2)	40.4 ± 3.3	40.5 ± 3.0	34.6 ± 3.2	35.3 ± 10.8	23.8 ± 2.1	28.1 ± 2.4

[a] BA: basal area.
[b] Mean ± SE.

TABLE 3

SUMMARY OF DISCRIMINANT FUNCTION ANALYSIS PERFORMED ON NEST SITE CHARACTERISTICS OF STARLINGS, SWALLOWS, BUFFLEHEADS, AND FLICKERS

Variables	Correlation between canonical vectors and variables		
	I	II	III
DBH	−0.270	0.214	−0.234
Canopy height	0.011	−0.889	−0.053
Nearest entrance obstruction	−0.142	−0.261	0.168
Nearest edge of stand	−0.077	−0.233	−0.875
Cavity volume	−0.987	−0.010	0.112
Entrance area	−0.490	−0.242	0.097
Eigenvalue	1.159	0.273	0.042
Percentage of variance explained	78.6	18.6	2.8
Canonical correlation	0.733	0.463	0.200

Correlations between the canonical vectors and the original variables were used to assess the importance of the original variables on each canonical axis as suggested by Williams (1983). The first axis was dominated by cavity volume, and to a lesser extent by entrance area. The second axis was strongly influenced by canopy height. Finally, the third axis was characterized by the distance to nearest edge of the stand (Table 3).

The DFA, however, resulted in only 62% of correct classification. Classification of starling and swallow cavities was relatively good (Table 4), however, Bufflehead cavities were classified as starling cavities almost as often as they were classified as Bufflehead cavities, and many flicker cavities were classified as starling cavities. The 95% confidence circles in Fig. 1 show that, according to our model, there was nearly total overlap

TABLE 4

CLASSIFICATION MATRIX OF NEST SITE CHARACTERISTICS USING STARLINGS, SWALLOWS, BUFFLEHEADS, AND FLICKERS BASED ON THE JACKKNIFE PROCEDURE[a]

Actual group	N	Predicted group (%)			
		Starling	Swallow	Bufflehead	Flicker
Starling	43	65	16	19	0
Swallow	31	13	77	3	6
Bufflehead	26	35	0	46	19
Flicker	14	14	0	36	50

[a] Overall percentage of groups correctly classified is 62%.

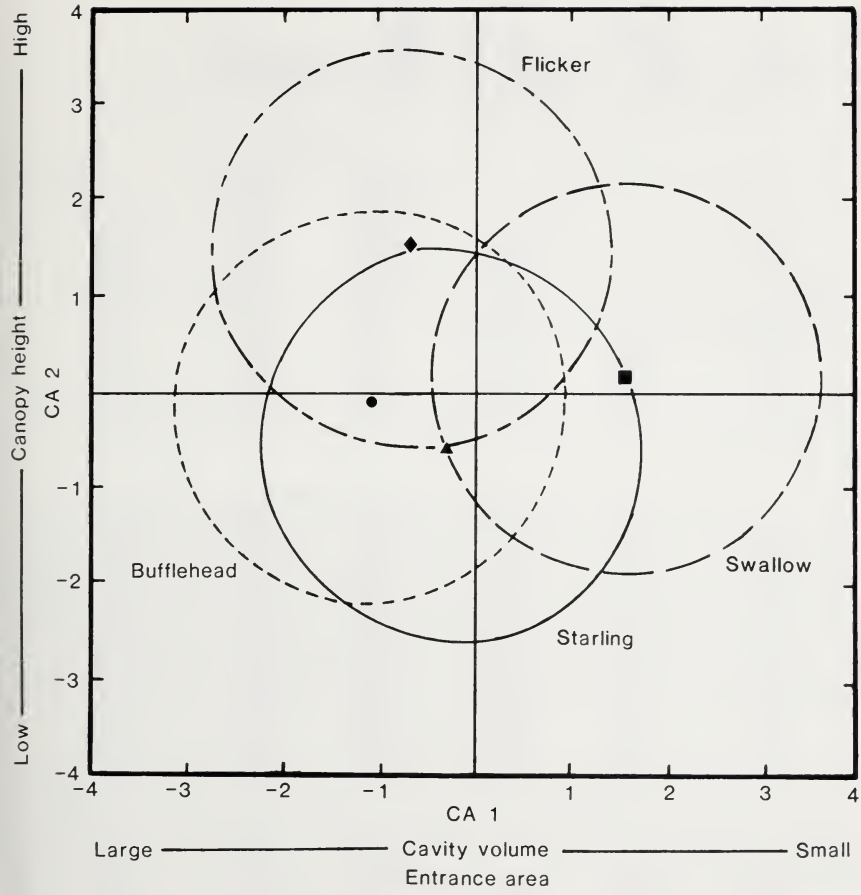

FIG. 1. Plot of centroids and 95% confidence circles of nest site characteristics for 4 species of cavity nesters on the first and second canonical axes.

between Buffleheads and starlings in cavity use. Flickers also overlapped with Buffleheads and starlings, whereas swallows overlapped less with flickers and Buffleheads.

As starlings have recently invaded this community, and as they showed the greatest overlap with other species in cavity use, we performed the DFA again using only swallows, Buffleheads, and flickers. The discriminant functions obtained were identical to those of the previous analysis; however, the accuracy of the classification improved to 82% (Table 5).

Comparison with previous data.—McLaren (1963) conducted a similar study in the same area 24 years ago, when starlings had just invaded the community. Although he had large sample sizes, his measurements were restricted to the cavity itself, thus limiting the extent of a comparison

TABLE 5

CLASSIFICATION MATRIX OF NEST SITE CHARACTERISTICS USING ONLY SWALLOWS, BUFFLEHEADS, AND FLICKERS BASED ON THE JACKKNIFE PROCEDURE[a]

Actual group	N	Predicted group (%)		
		Swallow	Bufflehead	Flicker
Swallow	31	90	3	6
Bufflehead	26	4	85	12
Flicker	14	14	29	57

[a] Overall percentage of groups correctly classified is 82%.

between the two studies. As McLaren's data included only flicker holes, we excluded individuals (mostly swallows) using sapsucker cavities from our data.

Cavity depths measured in this study differed from McLaren's data only for bluebirds, which used significantly deeper cavities (Fig. 2). The breadth of all flicker cavities was significantly smaller than in McLaren's data; however, there was no difference for any species taken separately, except for swallows, which had significantly narrower cavities. Finally, the entrance areas of our cavities were significantly smaller than in McLaren's data for all species but bluebirds, where the trend was similar.

DISCUSSION

Nest site characteristics.—Our data show that volume of the cavity and, to a lesser extent its entrance area, were the most important variables in determining species occupancy. Entrance size certainly limits cavity use by a particular species as there is a minimum size of hole that an individual can pass through. In addition, individuals may select the smallest hole possible to avoid eviction by a larger species or predation (Moed and Dawson 1979). It is surprising, however, that the volume of the cavity is more important than is entrance size in determining species occupancy. Zeleny (1977) and Moed and Dawson (1979) found that reproductive success in several species of birds was related to the inner cavity dimensions. They also found that cavity floor area affected clutch size, and that the depth of the cavity below the entrance was inversely related to losses owing to predation.

Why should height of the canopy, the dominant variable on the second canonical axis, be an important factor in determining cavity use? It is possible that canopy height influences access to the cavity, so that birds with low maneuverability prefer trees with a high canopy. Fig. 1, however, shows that flickers, which are the sole excavators of cavities in this group

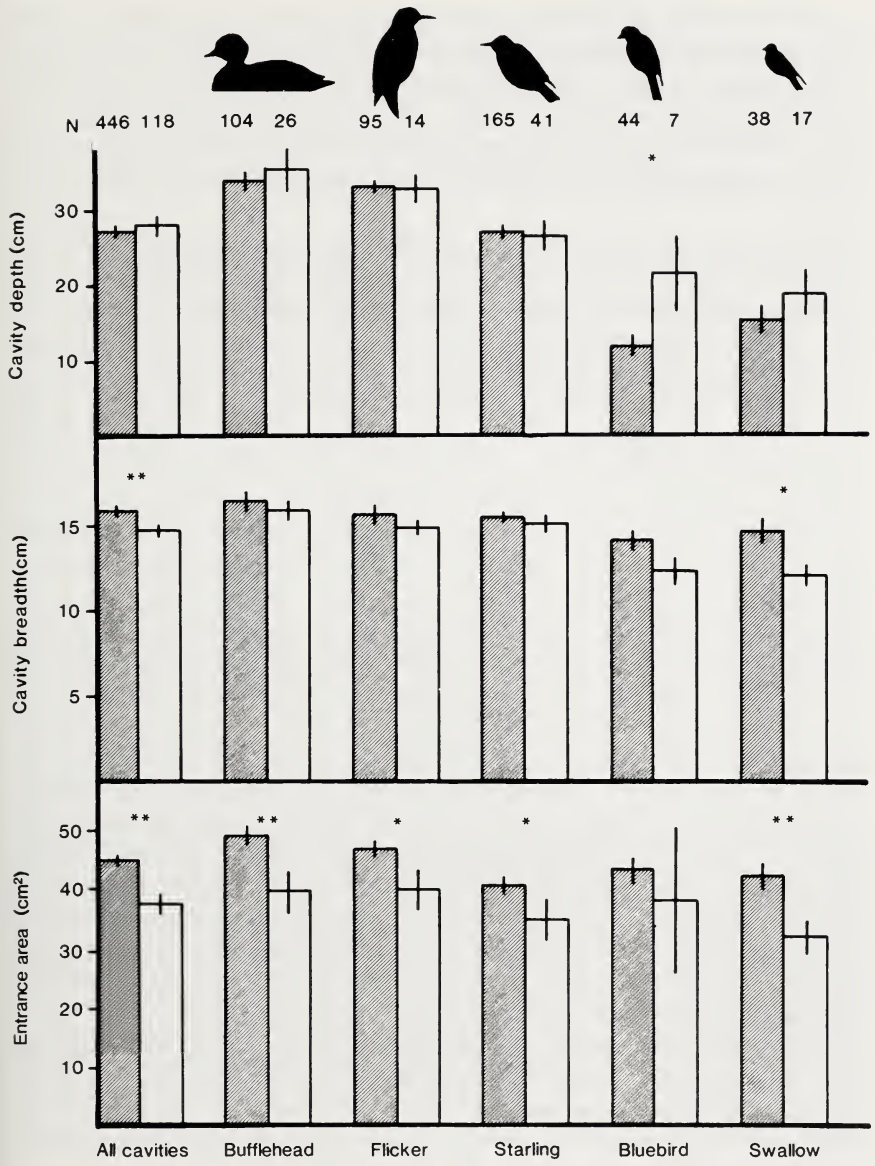

FIG. 2. Comparison of cavity dimensions found in this study (open bars) with similar data collected 24 years ago (calculated from McLaren 1963) (hatched) for 5 species of cavity nesting birds in the Cariboo parkland, British Columbia. Bird silhouettes are approximately scaled to relative body size. Mean ± SE (t test, * $P < 0.05$, ** $P < 0.01$, otherwise $P > 0.05$).

and thus should overlap the most with other species, are really the only species separated by canopy height. One explanation could be that cavities in high canopy trees are not available to secondary cavity nesters. We found that dead trees had a higher canopy than live ones (t-test, $P < 0.05$). The high canopy trees used by some flickers could have a shorter lifespan, falling earlier and thus becoming unavailable to secondary cavity nesters.

Interaction between starlings and other species.—The first record of starlings breeding in the Cariboo was in 1951 (Myres 1958). In 1959, McLaren (1963) found a large overlap in cavity use between starlings and other species. Erskine and McLaren (1976) later predicted that, because of competition with starlings, (1) flicker density would decrease, (2) cavities would become scarcer, and (3) competition for nest sites would intensify in this community. The percent of cavities occupied by starlings increased from 25% ($N > 450$, McLaren 1963) in 1959 to 44% ($N = 176$) in 1983. This suggests that starling populations have continued to increase and that competition for nest sites may have intensified. If competition has increased, we would expect a decrease in resource overlap among species (Mac Arthur 1972).

We looked at change in resource overlap by comparing our data with McLaren's data. The comparison suggests that some changes have indeed occurred in this community. The comparison is, however, limited in that data were collected by different observers in habitats that may have changed (e.g., through logging) in the past two decades. Fig. 2 shows that swallows and, to a lesser extent, bluebirds now use smaller cavities. Flicker cavities as a whole are also slightly smaller now, and these two species may merely be more opportunistic than others in their selection of nest sites. Alternatively, they may have been displaced from larger cavities by the more aggressive starling. This effect would be attenuated in swallows because they can use sapsucker cavities, a resource unavailable to other species. Bluebirds also use deeper cavities now, although the significance of this result is not clear to us.

Surprisingly, Buffleheads, which overlapped the most with starlings (Fig. 1), did not show any shift in cavity breadth or depth. We noted instances of Bufflehead nests being taken over by starlings (unpubl. data). Buffleheads, however, usually start nesting about 10 days before starlings and they may thus avoid being displaced by this species.

Cavities used in 1983 had a smaller entrance size than in 1959; however, all species were affected to the same extent, suggesting that the resource itself may have changed. Cavities excavated in Douglas fir last longer than those in aspens (Erskine 1978), and in fir trees the bark begins to rot before the tree falls, resulting in an enlarged cavity entrance (pers.

obs.). If McLaren's data included more fir cavities than ours (83% of our cavities were in aspen), this could account for the observed difference in entrance size. On the whole, cavity depth and breadth showed relatively little change compared to entrance size over the 24-year period between the two studies. This further strengthens the conclusion of the DFA that species have stricter requirements for inside cavity dimensions than for entrance size.

Despite the high overlap in cavity use, only 57% of the cavities found were used; however, the suitability of unused cavities was not assessed. Bluebirds and swallows tend to fill up cavities with nesting materials, making them unsuitable for species like Buffleheads and starlings (McLaren 1963). Unused cavities could have been older or more decayed as most aspens excavated for cavities have heartrot (Kilham 1971, Conner et al. 1976). Finally, some cavities may have remained unused because they fell within the territory of another individual. The distribution of cavities in our study was highly clumped (pers. obs.), and territorial species such as starlings, swallows, flickers, and bluebirds may have excluded conspecifics from suitable cavities.

It is not clear whether competition has intensified in this community despite the increase in starling abundance. Future research should quantify the availability of cavities in relation to their use by the different species.

SUMMARY

We studied nest site use by 6 species of cavity nesters in southcentral British Columbia. Discriminant function analysis was performed using nest site characteristics that differed significantly among 4 species (European Starlings, *Sturnus vulgaris*; Tree Swallows, *Tachycineta bicolor*; Northern Flickers, *Colaptes auratus*; and Buffleheads, *Bucephala albeola*). Cavity volume and, to a lesser extent, entrance area were the most important variables characterizing nest sites. Habitat variables were relatively unimportant except for canopy height, which also explained a significant amount of the variance. The analysis correctly classified only 62% of the cases, reflecting the high overlap in cavity use, especially between Buffleheads and starlings. We tested the prediction of Erskine and McLaren (1976) that competition for nest sites would increase in this community following its invasion by starlings 30 years ago by comparing nest site characteristics found in this study with similar data collected in 1959. Swallows now use significantly smaller cavities, bluebirds tend to use smaller but deeper cavities, and all species use cavities with a smaller entrance area. It is not clear, however, if these changes resulted from an intensification of competition or from a change in the resource available.

ACKNOWLEDGMENTS

This study was supported by the Canadian National Sportsmen's Fund and by a Natural Sciences and Engineering Research Council (Canada) grant to J. Smith. We thank S. Richards for assistance in the field, and M. Weston for her statistical assistance. J. Smith, J. Eadie, R. Conner, and T. Erskine critically reviewed this manuscript. We are also grateful to W. Monical for allowing us to work on his property.

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RAPTOR ORGANIZATION REGISTRY

Statement of Purpose: Raptor is here defined as including all species of the traditional avian orders Falconiformes and Strigiformes. To borrow a statement from the British Trust for Ornithology (BTO News; December 1978) concerning the purpose of this registry, it "is an exercise in communication." There are, in the world, numerous splendid organizations whose major purpose is to deal with some aspect of the life of raptors, unfortunately their number, location(s), and specific purpose(s) are unknown to organizations and individuals with the need to know. The Raptor Research Foundation is interested in identifying locations and purposes of as many of these organizations as possible. Your cooperation in accomplishing this task would be greatly appreciated. It is RRF's intent to (1) assemble a document compiling the results, (2) provide each responding organization with a copy of this compilation to facilitate communication, and (3) make it available to other organizations (e.g., wildlife, conservation, and funding agencies).

Officers of organizations dealing with some aspect of the life of raptors are asked to submit the following information for inclusion in "A Directory of Raptor Organizations of the World": official organization name, address (permanent address if there is one), brief statement of purpose, approximate number of members, major area(s) of interest (e.g., basic research, captive breeding of raptors, conservation, education, falconry, general aspects, raptor movement, rehabilitation), name and official position of responding individual. This information should be forwarded (on organizational letterhead if one is available) to

Richard J. Clark, Vice President
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Wilson Bull., 97(3), 1985, pp. 332–346

EFFECT OF VOLES ON MATING SYSTEMS IN A CENTRAL WISCONSIN POPULATION OF HARRIERS

FRANCES HAMERSTROM, FREDERICK N. HAMERSTROM, AND CHARLES J. BURKE

Polygyny has been reported among harriers (*Circus cyaneus*), and the circumstances under which it occurs have been the subject of some speculation. Before Balfour and Cadbury (1975) there were so few accounts of this phenomenon that it was deemed aberrant.

In North America, Reindahl (1941) found five harrier nests within a radius of half a mile. A male that defended two of these nests was believed to have mated with both females. Yocum (1944) reported two nests 400 yards apart in an 80-acre tract in Washington, both vigorously defended by one male. In Manitoba, Hecht (1951) observed unmarked birds at 11 nests, and clearly demonstrated that one male was a bigamist. Hamerstrom (1969) reported polygyny among color-marked harriers in Wisconsin.

In Britain, polygyny in Hen Harriers (*Circus c. cyaneus*) was first recognized in Orkney by J. Douglas in 1931 (Watson 1977), and seems to appear more frequently there following population increases (Balfour and Cadbury 1975, 1979). Polygyny has also been reported in Kincardineshire, Scotland (N. Picozzi, pers. comm. in Balfour and Cadbury 1975) and the Netherlands (van der Kraan and van Strien 1969). It has been suggested that polygyny in harriers may be the result of an unbalanced sex ratio in breeding adults both at Delta, Manitoba (Hecht 1951), and in Orkney (Balfour and Cadbury 1975, 1979).

In this paper we discuss mating systems of *C. c. hudsonius* in Wisconsin and show that polygyny is not aberrant but occurs regularly, and further that it is tied to vole (*Microtus pennsylvanicus*) abundance.

STUDY AREA

The study area is in and on the edges of the Buena Vista Marsh, in Portage County, and the northern part of the Leola Marsh in Adams County, Wisconsin. It encompasses 51,830 acres (20,732 ha), subdivided into two parts, the core area and the periphery (Fig. 1). The core area consists of the best nesting habitat, and all but three nests found since the study began in 1959 have been within it. The core area totals 41,718 acres (16,687 ha) and corresponds to the figure of "approximately 40,000 acres" that has been used in earlier papers and theses (e.g., Hamerstrom 1969). The peripheral zone of 10,112 acres (4045 ha) is less clearly defined and is used by harriers mainly for hunting.

Farming is common on both the sandy interior islands and edges and on the muck and peat of the two drained marshes. The lowest areas tend to become sedge (*Carex* spp.) and

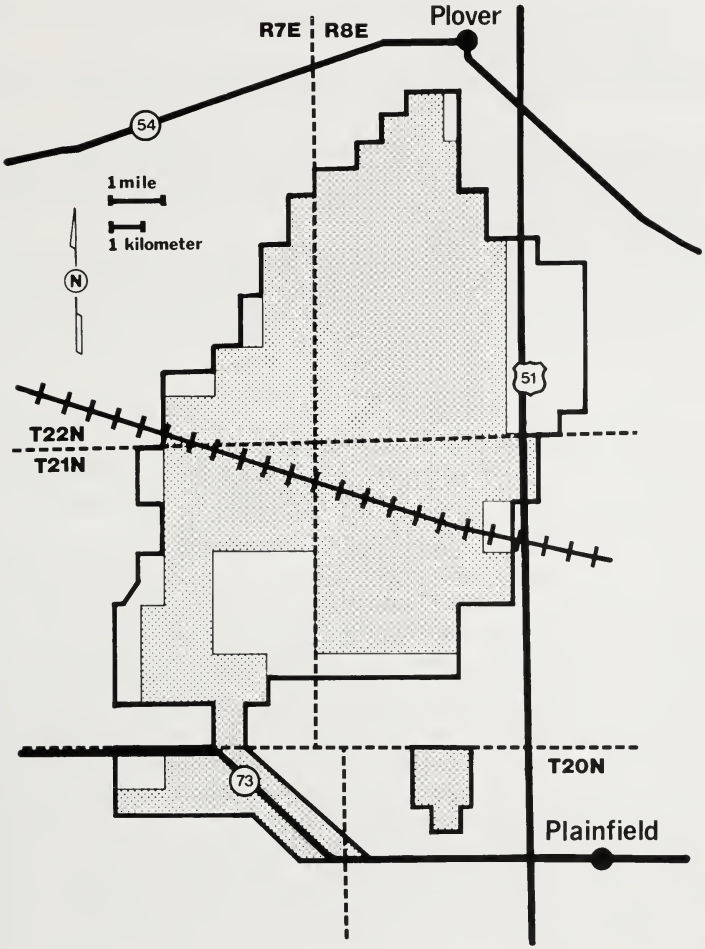

FIG. 1. The study area. The "core area" is stippled; the rest, inside the heavy boundary line, is the "peripheral area." The railroad crossing the area is now abandoned.

willow (*Salix* spp.) swales. For a more detailed description, see Hamerstrom and Hamerstrom (1973).

Approximately 11,377 acres (4551 ha) are managed as grasslands for the Greater Prairie Chicken (*Tympanuchus cupido pinnatus*), with important repercussions for the harrier (Hamerstrom 1974).

METHODS

The study began in 1959, when only part of the area was searched for nests. Full coverage began in 1960 and continued through 1983. Data for 1959 are usable for *totals*—e.g.,

numbers of nests and young—as in Tables 1–3, but are excluded from comparisons among years, e.g., Table 4 and all figures.

Banding, with U.S. Fish and Wildlife Service bands, and color marking have been critical elements in the study, both for keeping track of individuals in the field and in the analysis of data.

Trapping techniques.—In spring, before harriers were on breeding territories, we used bal-chatris baited with European Starlings (*Sturnus vulgaris*) (Berger and Hamerstrom 1962). Breeding adults were caught in a dho-gaza over a stuffed or live tame Great Horned Owl (*Bubo virginianus*) (Hamerstrom 1963).

We devised a new method of trapping breeding adults that were poor reactors to the dho-gaza set. A "nest dome" was placed over the young in the nest. The nest dome is flattened quonset-shaped, measures 63 × 18 cm at the base and 27 cm high, and is made of 1 in. welded wire with about 200, 40-lb test monofilament nooses, 5 cm in diameter, tied to its top. In essence, the nest dome acts as a bal-chatri with the nestling harriers as bait.

Banding and color marking.—Breeding adults were aged, sexed, weighed, measured, banded, and color marked. Colored feathers imped into the wings enabled us to recognize individuals with the unaided eye at distances up to 0.4 km (Hamerstrom 1969). After 1961, all breeders were also given colored jesses, which enabled individual recognition in later years without retrapping. The jesses were made of brightly colored strong plastic, and were attached around the tarsi with rivets.

In all, 231 breeding harriers were banded, 220 of which were also color marked. An additional 70 incoming or passage birds were banded in spring and not retrapped as breeders; 57 of these were imped but none was jessed. Six hundred forty-seven nestlings were sexed, measured, aged, and banded but not color marked.

Nest finding.—Harriers were watched with spotting scopes and binoculars. Methods of nest finding are described in Hamerstrom (1969). After the first few years, because we feared that harriers would desert if nests were disturbed during incubation, we normally made our first nest visits after the eggs had hatched. As a result, some nests that failed before hatching may have been missed. Except in 1959, all successful nests (i.e., nests in which at least one young fledged) were found, either before the young had fledged or, in some cases, after fledging when the young are conspicuous and remain in the close vicinity of their nests for several weeks (Hamerstrom 1969). Including the latter, 330 nests have been found. By our definition, a nest had to contain an egg or evidence that an egg had been present. We made five exceptions to this rule, one in 1962 and four in 1969; all were parts of polygynist menages. In each case, the behavior of the female led experienced observers to be confident that nests actually were present.

Marked individuals enabled identification of monogamous and polygynous birds. Polygynous males were those that fed or defended nests with two or more females.

Sixteen of 27 bigamous males were color marked; 11 bigamist males could not be trapped but were identified by plumage. Of 54 females involved in bigamy, 35 were color marked; 19 could not be trapped but were seen accepting food transfers from or having their nests defended by known bigamist males.

Of eight trigamous males, seven were color marked. One could not be trapped but was seen feeding three (two color marked and one unmarked) females within one hour. Fifteen of 24 females involved in trigamy were color marked; nine were not, but were seen accepting food from or having their nests defended by a known trigamist male.

Potential breeders, nonbreeders, sex ratio.—A determined effort was made to find non-breeders. At least two trained observers covered the marshes from early June, after the incoming migrants had settled in, until early July when a small influx of harriers from other areas is to be expected. Each observer tallied or mapped his sight records independently,

after which a consensus was reached as to total numbers of potential breeders—the summer population—and sex ratio. Agreement was generally within two or three birds. These tallies were aided by marked birds, some imped in spring, and some color jessed in earlier years. The actual breeders and the nonbreeders were sorted out as the summer progressed.

Vole index.—An index to vole abundance has been conducted since 1960 (Hamerstrom 1979). From 1960 through 1967 D. Q. Thompson (pers. comm.) provided an index to regional vole abundance based on stems cut by voles in Wisconsin and neighboring states; in 1964 we began a local index based on break-back trapping, using peanut butter as bait, on the study area. An objective of 1080 (1200 after 1972) trap nights per breeding season has been met or exceeded each year except 1969 (745 trap nights). The curve shown in Figs. 2 and 3 is derived from the number of voles caught each year, divided by the number of trap nights, multiplied by 1000. (This is the actual formula used in Hamerstrom 1979:371, rather than the formula given there; the 1979 graph itself is correct.)

RESULTS AND DISCUSSION

Most harriers were monogamous, but polygyny played a consistent role. To understand fully the mating systems of the central Wisconsin harrier population, however, one must go beyond vital statistics and look at the relationship between harrier nesting and vole abundance.

Number of nests and nesting success.—We do not know exactly when the first vole cyclic period (ca 1960–1964) began, and it is less clearly defined in that we used a regional, rather than the later local, vole index (Figs. 2 and 3). There seem to have been three moderate peaks of vole abundance during this first period, at least one of which, 1963, we believe to be well documented (see Hamerstrom 1979). The still incomplete last period shows a plateau in 1981–1983 rather than a rise to a high.

The years 1960–1978 have been detailed in Hamerstrom (1979). We now add another peak and plateau in numbers of both voles and harrier nests (Figs. 2 and 3). Except for the aberrant low number of nests in 1966, which we attribute to DDT, the correlation between the numbers of voles and harrier nests is at once obvious. In a way, the two plateaus in nesting at intermediate vole numbers (1977, 1978, 1981–1983) are even more convincing than the highs and lows: the two periods of intermediate vole abundance are faithfully mirrored by numbers of harrier nests.

Two hundred fifty-two of 330 nests (76%) were of monogamous pairs (Table 1). Monogamy was thus the more common situation and the only one to occur every year (Fig. 3). Monogamous nests were more successful (76%) than polygynous nests (64%), and they fledged the greatest number of young in total (588 of 726) and per female (2.3); successful monogamous females averaged 3.1 young (Table 1).

There were 27 instances of bigamy and eight of trigamy during 15 of the 25 years. Trigamy occurred without bigamy only in 1970. Bigamous matings occurred in 14 years and fledged 100 young; trigamous matings

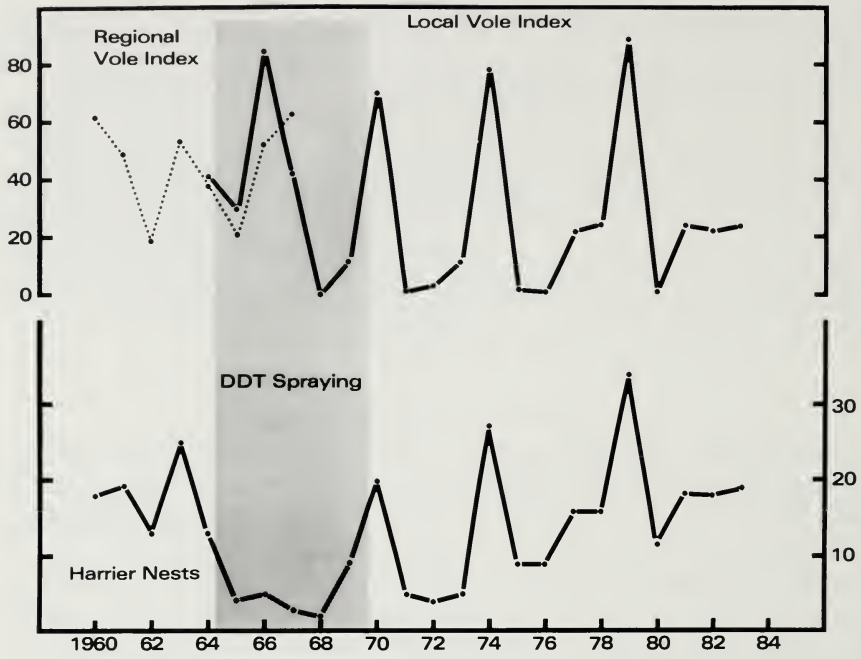

FIG. 2. Harrier nests in relation to vole abundance, 1960–1983.

during six years fledged 38 young. Bigamous females were less successful than trigamists (61% vs 71%) in terms of nests that fledged at least one young, but averaged higher productivity per female (1.9 vs 1.6 young); the number of nests, however, is small (Table 1).

Alan Beske (pers. comm.) kept track of a radioed male trigamist that mated with three females, all of whose nests were found, and that also copulated with a fourth female. No nesting resulted in this last instance, and we have not included the fourth female in our calculations.

Number of potential breeders.—Except for two years, there were always more potential breeders than actual nesters. In 1974 and 1979, both years with many nests, the estimated number of potential breeders equalled the number of actual breeders. Of the two years, 1979 was the year with the highest-ever number of polygynous nests, 21, as against two in 1974. Both 1979 and 1974 were high vole years (Fig. 3). In short, neither the annual number of nests nor the extent of polygyny seems to have been caused by a shortage of potential partners.

Sex ratio.—The sex ratio of the population might be expected to influence breeding behavior, and the occurrence of monogamy and polygyny.

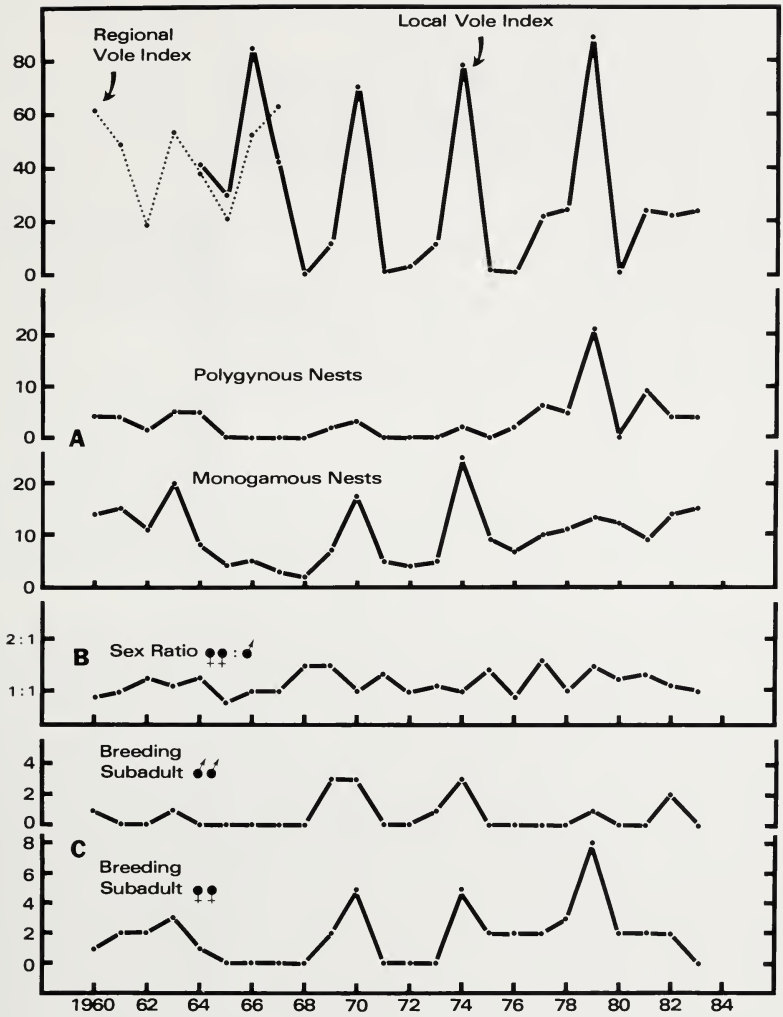

FIG. 3. Harrier vital statistics shown in relation to vole abundance: A. incidence of polygyny and monogamy; B. sex ratio; C. nesting by subadults.

In harriers the two sexes do not appear to contribute equally to the nesting effort. The female lays and incubates the eggs; the male brings most of the female's food during incubation and shortly after the eggs hatch, then both bring food to the nestlings; but only the female tears it into pieces small enough for helpless young to swallow. Some males desert before the young are fully fledged. There are many instances of abandoned females successfully fledging young, but we have only one example of a

TABLE 1

HARRIER BREEDING PERFORMANCE IN RELATION TO MATING SYSTEM, 1959–1983

	Monogamy	Bigamy	Trigamy	Total
Number (%) of all nests	252 (76)	54 (16)	24 (7)	330
Percent of nests successful[a]	76	61	71	73
Number of successful nests:				
Per female	0.8	0.6	0.7	0.7
Per male	0.8	1.2	2.1	0.8
Percent of males successful	76	85	100	77
Number (%) of young fledged	588 (81)	100 (14)	38 (5)	726
Mean ± SD per female[b]	2.3 ± 1.6	1.9 ± 1.7	1.6 ± 1.5	2.2 ± 1.7
Mean ± SD per successful female	3.1 ± 1.1	3.0 ± 1.0	2.2 ± 1.3	3.0 ± 1.1
Mean ± SD per male	2.3 ± 1.6	3.7 ± 2.4[c]	4.8 ± 1.7[d]	2.5 ± 1.8
Mean ± SD per successful male	3.1 ± 1.1	4.4 ± 2.0	4.8 ± 1.7	3.3 ± 1.3

[a] Successful nests fledged at least one young. In addition to young seen on the wing, birds banded shortly before fledging time were presumed to have fledged.

[b] Number fledged per nest ranged from one to five in all mating systems. Five young were fledged by 8% of monogamous pairs, but by only 2% of bigamous nestings and 4% of trigamous nestings.

[c] Range 1–8.

[d] Range 2–7.

TABLE 2

BREEDING PERFORMANCE OF MONOGAMISTS, AGE OF BOTH PARTNERS KNOWN, 1959–1983[a]

Age of females	Subadult males	Adult males	Total
Subadults[b]			
Number of nests	4	22	26
Percent of nests successful	100	82	85
Number of young fledged	11	56	67
Mean ± SD per female	2.8 ± 1.3	2.6 ± 1.7	2.6 ± 1.6
Mean ± SD per successful female	2.8 ± 1.3	3.1 ± 1.2	3.0 ± 1.2
Adults			
Number of nests	8	123	131
Percent of nests successful	62	78	77
Number of young fledged	13	320	333
Mean ± SD per female	1.6 ± 1.4	2.6 ± 1.7	2.5 ± 1.7
Mean ± SD per successful female	2.6 ± 0.6	3.3 ± 1.0	3.3 ± 1.0

[a] Ninety-five nests, involving 40 males and 75 females for which the age of only one partner is known, are omitted (including four subadult males and four subadult females).

[b] Subadults are birds that hatched the year before. Adults are birds that hatched at least two years before.

male fledging young after disappearance of the female; those young were old enough to tear food for themselves when left motherless.

Over the 24-year period 1960–1983, the ratio of females to males among the potential breeders was 1.1:1, with a range of 0.8–1.6:1 (Fig. 3). The year-to-year variation shows no relationship to vole numbers (Fig. 3).

Polygyny occurred in eight years when there was an excess of females among potential breeders. The highest incidence was in 1979, when the ratio of females to males was 1.5:1; however, only three of those eight years were conspicuously above an even sex ratio, and four above-even years showed no polygyny (DDT years are excluded). There were seven years when the sex ratio was 1:1 or lower, but in which polygyny nevertheless occurred. Clearly, polygyny was not caused by an excess of females.

Age of breeding birds.—The role of subadults (birds hatched the year before) in breeding populations of harriers has only recently come to light (Hamerstrom 1969, Balfour and Cadbury 1979). During 24 years of study in Wisconsin, 60 subadults bred, 16 males and 44 females. To distinguish between adult and subadult females during the breeding season, one must determine eye color (i.e., either catch the bird, or get close enough to it to see eye color) (Hamerstrom 1968). Because we were not always able to do this, some females were not aged. However, of those females that were recognizably subadults, we know of none that was not breeding. It is thus quite possible that most Wisconsin females breed at one year.

TABLE 3

BREEDING PERFORMANCE OF POLYGYNISTS, AGE OF ALL PARTNERS KNOWN, 1959–1983[a]

	Bigamy		Trigamy	
	Subadult females	Adult females	Subadult females	Adult females
Number of nests	10	25	4	13
Percent of nests successful	60	76	50	92
Number of young fledged	16	61	3	27
Mean ± SD per female	1.6 ± 1.6	2.4 ± 1.7	0.8 ± 0.8	2.1 ± 1.2
Mean ± SD per successful female	2.7 ± 1.0	3.2 ± 1.1	1.5 ± 0.5	2.3 ± 1.1
Mean ± SD per male	—[b]	4.5 ± 2.4	—[c]	5.5 ± 0.7
Mean ± SD per successful male	—	5.1 ± 1.8	—	5.5 ± 0.7

[a] Fifteen bigamous and seven trigamous nests, accounting for 16 and eight young, respectively, have been excluded because the females were not aged. Four bigamous nests (seven young) have been excluded because their two males were not aged. All males in the table were adults.

[b] No polygynous males were known to have had only subadult mates. Five adult males with one subadult and one adult female each averaged fewer young (4.3 ± 2.6 per successful male) than the eight with two adult mates (5.1 ± 1.8 per successful male).

[c] For only two males (both adults) could all three females (all adults) be aged. Failed nests gave fewer chances to determine the female's age, biasing the results toward apparent failure. All harems with females of unknown age are therefore omitted; three of them did include subadult females.

It is difficult to assess the importance of age in relation to nesting and nesting success, for the members of a monogamous pair or polygynous menage were often not of the same age. In a few cases, the age of all partners was known. Among 157 such monogamous pairs there were 4 pairs of breeding subadults all of which were successful (Table 2). There is an indication that productivity increased with age, especially among monogamous males. Subadult females fledged fewer young when mated with trigamist males than with bigamists (Table 3) and those mated with bigamists fledged fewer young than those mated with monogamists (Table 2). Productivity of polygynous males varied erratically in our small samples, but averaged highest for both bigamist and trigamist males when they were mated with adult females.

Individual nesting success, whether or not the age of the partner(s) was known, for 44 subadult females was slightly lower than that for 171 adults (75% and 78%, respectively); the number fledged per successful nest was similarly close (2.8 and 3.1, respectively). In short, we find few substantial age-related differences among females in nesting success or fledging rates. This was not so with the males. Despite the almost even sex ratio, fewer males than females bred in their first year (16 vs 44). None were polygynists. Subadult males nested in only 9 of the 24 years, as opposed to 16 of 24 years for subadult females (Fig. 3). They did, however, show a high rate of nesting success, 88%.

Effect of voles on population structure.—In order to deal with our best data on "normal behavior," we here omit all but 1963 of the first cyclic period and the aberrant DDT years, 1965–1968. We include 1969 because the harrier population was then beginning to recover. During this period of best data, vole abundance powerfully affected the occurrence of polygyny (Fig. 3). Polygyny occurred at all four vole highs—averaging 7.8 nests per high—and during each of the five years of intermediate vole abundance with an average of 5.6 nests. During the seven low years, however, polygyny occurred only twice, with only two nests each time. Monogamous nesting generally increased even more sharply at the vole highs but there was a curious exception in 1979, when monogamous nests rose only to 13 as compared to their highest number, 25, while polygynous nests numbered 21, far above their next highest, 9.

Nesting success during the 16 years under discussion was highest during vole highs but not strongly so, averaging 78% during the four vole highs, 71% during the five intermediate years, and 75% during the seven low years. The number of young fledged per successful nest was essentially the same during vole highs (3.0 ± 1.1), in intermediate years (2.8 ± 1.1), and at vole lows (3.1 ± 1.1); the average for these 16 years and for the entire study was 3.0 ± 1.1. Total annual production of young followed the vole index very closely.

Table 4 records our data for these 16 "best" years to show the performance of known-age females in relation to both vole numbers and type of mating system. The samples are so small that the data are no more than suggestive, but it is the largest body of such data at present available and should be useful as a starting point for later studies. The relative scarcity of polygynous females, and especially subadults, at vole lows, is apparent. For monogamous females nest success was essentially the same at lows and highs, with some increase during intermediate years. Polygynous adults showed increasing nesting success from lows to highs (67% during lows, 79% during intermediate years, 100% during highs); however, the average number of young fledged per successful female was highest during the lows (3.5 ± 0.7). Among adult females, average production of successful monogamists and polygynists differed by no more than 0.3 young (Table 4).

In short, high vole numbers led to (1) first and foremost, a marked increase in the total number of harriers nesting in a given year; (2) an increase in the number of subadults nesting; and (3) an increase in polygyny. These effects were far more pronounced than changes in nesting success or the number of young fledged.

The polygyny threshold model.—Polygyny was an advantage to participating males: more young were fledged per male and the chance of being

TABLE 4

NESTING OF KNOWN-AGE FEMALES, AGE OF PARTNER NOT ALWAYS KNOWN, IN RELATION TO VOLE ABUNDANCE[a]

	Low years		Intermediate years		High years	
	Subadults	Adults	Subadults	Adults	Subadults	Adults
Number of nests						
Monogamous	7	19	4	39	12	40
Polygynous	1	3	5	14	8	12
Percent of nests successful						
Monogamous	86	79	75	87	92	80
Polygynous	100	67	40	79	63	100
Number of young fledged						
Monogamous	19	50	7	98	35	104
Polygynous	3	7	5	28	11	36
Mean ± SD fledged						
Per female						
Monogamous	2.7 ± 1.7	2.6 ± 1.6	1.8 ± 1.5	2.5 ± 1.4	2.7 ± 1.3	2.6 ± 1.7
Polygynous	3.0 ± 0.0	2.3 ± 2.1	1.0 ± 1.4	2.0 ± 1.5	1.4 ± 1.5	3.0 ± 1.3
Per successful female						
Monogamous	3.2 ± 1.3	3.3 ± 0.9	2.3 ± 1.2	2.9 ± 1.0	2.9 ± 1.1	3.3 ± 1.1
Polygynous	3.0 ± 0.0	3.5 ± 0.7	2.5 ± 0.7	2.6 ± 1.1	2.2 ± 1.3	3.0 ± 1.3

[a] The vole index is a measure of vole abundance: an index of less than 15 is a low year, 15–45 an intermediate year, more than 45 a high year. See Figs. 2 and 3. The table summarizes the 16 years of "best" data: see text for details.

a successful breeder increased numerically (Table 1). For individual females, however, the chance of successful breeding decreased, as did the number of young fledged. Balfour and Cadbury (1979) found that male Hen Harriers in Orkney mated to 3–4 females brought off more young than monogamous males.

Both Hecht (1951) and Dent (1939) were able to identify females in polygynous groups that were favored by their males and were apparently dominant over the other females. Newton (1979) has discussed such "alpha females" in detail. We have occasionally recognized favoritism in polygynous groups, but have been unable to detect a stable female hierarchy. The logistics of our field work has kept us from learning the order in which females settled in a polygynous male's territory. In most cases polygyny has been simultaneous, rather than serial, for most of the nesting period.

Oring (1982) has summarized the considerable amount of research in recent years on polygyny, most of it on passerines. He adduces three kinds of polygyny: (1) resource-defense polygyny, in which males defend resources critical to female reproductive success, such as food and cover; (2) direct defense of grouped females; and (3) male-dominance polygyny, based on competition, which allows females to choose on the basis of male quality (not otherwise defined). We cannot place harrier polygyny within this scheme because we have so seldom seen any evidence of territorial defense, defense of mate, or male-male tests of dominance through fighting or even a show of aggression. In fact, territoriality in the harrier has not been well defined, and its influence on breeding behavior is obscure. Harriers defend their nests (or nest area) against other species (including man), but defense against conspecifics has been less well documented. We have found few specifically described instances of it (Errington 1930, Watson 1977:125–126, Craig et al. 1982) and have seen no clear evidence ourselves. By inference, a mechanism for conspecific territoriality probably exists, but it must be remarkably subtle. For the present, we speak of territory as the area near the nest defended against intruders.

Darwin (1871) suggested that the choice of mate is made by the female. Under what conditions does a female choose a male that is already mated? Assuming that the best habitat has already been usurped, she may do better with an already mated male on superior habitat than with a monogamous male on inferior habitat, where her chance of success may be lower (Orians 1969); "monogamy with a pauper vs. polygyny with a tycoon" (Mock 1983). This difference in quality of habitats is a key factor, and is described as the "polygyny threshold" (Verner and Willson 1966, Garson et al. 1981). Furthermore, polygyny is expected to evolve only

when this difference in quality of habitats regularly presents itself (Orians 1969).

Once a female harrier is incubating, the male usually does essentially all the hunting. During incubation, females rarely leave the nest except for food transfers and brief periods of preening and flying. When voles are scarce, a male with one incubating female may be able to transfer food to her only two or three times a day (K. L. Bildstein, pers. comm.). But during high vole years males are able to present food more frequently—or to more females.

In 1979, during a vole high, we sometimes saw polygynous males circling above their nests calling to the females in what appeared to be attempts to draw them off the nest to accept food. But the incubating females, presumably sated, did not leave their nests. After failing to call the female off, the males usually flew to nearby perches. There they tore at the food, sometimes eating it, called to the female, or made short flights around the nest area. It is likely that unmated females may recognize such behavior as an index of the high quality of the male's territory.

In fact, 18 times (23%) successful females in polygyny fledged more young than the average number fledged by successful monogamous females for a given year, although monogamous females were generally more productive. This suggests that those harem females had indeed selected superior males or superior habitat.

There is need for a closer study of polygyny in harriers, but our data suggest that harriers fit the polygyny threshold model, with voles as the key factor. This would seem to be Oring's (1982) resource defense type of polygyny, but the mechanism of defense is not clear.

SUMMARY

This 25-year study on a 51,830 acre (20,732 ha) area in central Wisconsin is based on 231 banded breeding harriers (*Circus cyaneus hudsonius*), 330 nests, and 726 fledged young of which 647 were banded. Harriers were most commonly monogamous but polygyny (including both bigamy and trigamy) accounted for 24% of the nests and 19% of young fledged. Polygynous males sired more young than monogamous males. The reverse was true of harem females. The number of harrier nests closely mirrored the course of the vole (*Microtus pennsylvanicus*) population cycle, except during a period (1965–1968) of heavy aerial spraying of DDT. Vole abundance, not an excess of females or shortage of breeders, also triggered increased polygyny. Subadult females commonly bred and were involved in polygyny when voles were abundant. Subadult males bred less commonly than subadult females, and were never polygynists; they, too, bred more often during periods of vole abundance but to a lesser degree than subadult females. The data fit the polygyny threshold model with vole abundance a key factor. In short, the abundance of the prey—voles—governed not only the abundance of the predator, but also its mating systems.

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COMPARATIVE HABITAT USE BY LOUISIANA AND NORTHERN WATERTHRUSHES

Robert J. Craig

Discovering distinctive structural features that characterize the habitats of avian species has been an important goal of researchers (Hespenheide 1971, Noon 1981, Collins 1983). Vegetation structure is frequently thought to predominate in avian habitat selection (MacArthur 1971, Collins 1983), but floristic (e.g., Holmes and Robinson 1981) and physical (e.g., Kendeigh and Fawver 1981) variables can also influence habitat associations.

An additional factor thought to influence habitat use by coexisting, ecologically similar species is interspecific competition. Through competition, species might be expected to diverge in habitat use (Morse 1980). Recent studies, however, suggest that interspecific competition does not always occur between similar species (Morrison 1981, Frakes and Johnson 1982, but see Robinson 1981).

Here, I examine the breeding habitats of the Louisiana (*Seiurus motacilla*) and Northern (*S. noveboracensis*) waterthrushes to determine whether their habitats possess distinctive features, and to learn whether overlap in habitat use leads to interspecific competition. Bent (1953) and Eaton (1957, 1958) qualitatively described waterthrush habitats, but there are only limited data (Vassalo and Rice 1982, Swift et al. 1984) concerning the quantitative structure of habitats used by the two species.

STUDY AREAS AND METHODS

Habitats.—I studied habitat use in waterthrushes in northeastern Connecticut from 1978 to 1980 and in 1984, principally in a rocky ravine, Boston Hollow, in Yale Forest, Ashford, Tolland Co. Both species nest in the wooded wetlands extending 1.6 km along the floor of the ravine. In addition, I made qualitative evaluations of habitat at 26 other Connecticut locations.

The wetlands of Boston Hollow have a forest canopy of yellow birch (*Betula lutea*), black ash (*Fraxinus nigra*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), eastern hemlock (*Tsuga canadensis*), and white pine (*Pinus strobus*), with conifers predominating in most swamps and deciduous cover predominating along most streams. Speckled alder (*Alnus rugosa*) often reaches sapling size. Shrubs include black alder (*Ilex verticillata*), sweet pepperbush (*Clethra alnifolia*), spicebush (*Lindera benzoin*), and speckled alder. Typical herbs are cinnamon fern (*Osmunda cinnamomea*), sensitive fern (*Onoclea sensibilis*), and skunk cabbage (*Symplocarpus foetidus*).

Morphology.—I identified most individuals in the field by netting and color banding adults. Netted birds were sexed, weighed, and measured (wing chord and tail length). I calculated the relative wing and tail length of each bird by dividing the cube root of body mass, a linear index of body size, into wing and tail measurements.

Habitat structure.—Of 37 territories found at Boston Hollow over four years, I compared habitat data from 10 territories of each species. Because some territories were located similarly to those of previous years and many adults returned to breed in subsequent years, I did not select territories for analysis randomly. Rather, I included as many different sites and individuals as possible to minimize redundancy of observations. Of the 10 Northern Waterthrush territories studied six were overlapped (73–100%) by those of the 10 generally longer Louisiana Waterthrush territories (see map in Craig 1984).

I assessed herb, substrate, and water cover by dividing every territory into five "blocks." In each block I randomly placed a 20-m transect with sampling points every meter (100 total points). At each point I noted the identity of herbs present, presence of moss, type of substrate (mud and leaf litter, rock, root, or log hummock), and occurrence of water. I also distinguished between fast-moving water, which causes surface ripples, and slow-moving water, which does not cause ripples.

I measured shrubs on separate 20-m transects with sampling points every 2 m (50 total points). To estimate crown cover I counted the times shrub species touched a vertical 3-m pole on each of the pole's 1-m sections (Mueller-Dombois and Ellenberg 1974).

To study tree cover, I placed a transect with five points 10 m apart in each of four blocks and measured trees with a minimum height of 6 m and a minimum circumference of 10 cm. For each tree species I calculated an importance value, a relative index of density, frequency of occurrence, and basal area per ha, which provides a measure of proportional representation of forest foliage (Holmes and Robinson 1981). From field data I also calculated trees/ha and mean basal area. I determined sample size for all analyses with Stein's two stage sample (Steele and Torrie 1960).

Because territory sizes differed (Craig 1984), equal sampling effort yielded estimates with different associated variances. For data that were not normally distributed, I used the non-parametric Wilcoxon's two sample test (Steele and Torrie 1960). For the normally distributed morphometric data, I used Student's *t*-test.

RESULTS

Habitats.—At Boston Hollow I found little interspecific difference in total herbaceous cover of territories, and territories of the two species widely overlapped in all features measured (Table 1). In the principal structural classes present, forbs and ferns, territories of Northern Waterthrushes had significantly fewer forbs and significantly more ferns than those of Louisiana Waterthrushes. Lower density of herbs such as *Lycopus, Viola,* and *Sium* resulted in less forb cover, and a much higher density of *Osmunda* was largely responsible for the greater fern cover. A third structural class, coarse herbs (composed solely of *Symplocarpus*), showed no significant interspecific territorial difference. Territories of Northern Waterthrushes had significantly more moss cover than those of Louisiana Waterthrushes.

The ratio of water to ground surface was similar in territories of the two species, as were percent mud and leaves and percent slow-moving water (Table 2). Differences occurred in area of fast-moving water, which was significantly greater in Louisiana Waterthrush territories, and in number of hummocks, which was significantly greater in Northern Water-

TABLE 1
PERCENT HERBACEOUS COVER IN WATERTHRUSH TERRITORIES

Cover	Louisiana Waterthrush	Northern Waterthrush
Osmunda cinnamomea	6.7 (0–19)[a]	21.4 (2–39)*
Onoclea sensibilis	8.7 (0–27)	10.3 (1–21)
Symplocarpus foetidus	9.2 (0–33)	6.2 (0–37)
Total forbs	17.4 (11–23)	12.5 (4–21)*
Total ferns	17.9 (7–29)	31.9 (12–53)**
Total herbs	40.7 (21–76)	47.3 (30–66)
Moss	19.9 (8–35)	34.6 (5–46)*

[a] Mean with range in parentheses (N = 10).
* Species differ at $P < 0.05$, Wilcoxon test.
** Species differ at $P < 0.01$, Wilcoxon test.

thrush territories. Again, territories of the species overlapped in all substrate features measured.

Territories of Northern Waterthrushes had significantly higher total shrub density and higher densities of shrubs in the 1–2 and 2–3 m height classes compared with those of Louisiana Waterthrushes (Table 3). Much of the difference between species was attributable to significantly more evergreens (sapling *Tsuga*) in Northern Waterthrush territories. In contrast, total deciduous density as well as density of individual deciduous species differed only slightly between the species. As in the case of herbs, territories varied widely and much interspecific overlap occurred.

Mean basal area of trees, a measure of trunk size, differed only slightly between territories of the two species, but significantly more trees/ha and a higher evergreen-to-deciduous ratio occurred in the territories of Northern Waterthrushes (Table 4). The importance value (IV) for *Tsuga,* the

TABLE 2
PERCENT COVER BY WATER AND TERRESTRIAL SUBSTRATES IN WATERTHRUSH TERRITORIES

Cover	Louisiana Waterthrush	Northern Waterthrush
Fast water	23.7 (5–56)[a]	3.8 (0–13)**
Slow water	22.9 (4–42)	31.6 (14–51)
Hummocks	30.9 (13–48)	45.8 (12–61)*
Mud and leaves	21.5 (3–44)	17.4 (6–61)
Water/ground	1.1 (0.4–2.9)	0.6 (0.3–1.1)

[a] Mean with range in parentheses (N = 10).
* Species differ at $P < 0.05$, Wilcoxon test.
** Species differ at $P < 0.01$, Wilcoxon test.

TABLE 3
DENSITY OF SHRUB CROWNS IN WATERTHRUSH TERRITORIES

Substrate	Louisiana Waterthrush	Northern Waterthrush
Ilex verticillata	62.8 (17–106)[a]	95.5 (24–162)
Clethra alnifolia	10.0 (0–23)	19.6 (0–82)
Lindera benzoin	11.2 (0–33)	3.1 (0–9)
Tsuga canadensis	34.6 (0–115)	71.1 (1–106)**
Total deciduous	112.6 (86–166)	136.3 (56–182)
Height classes:		
0–1 m	32.4 (16–59)	28.4 (7–46)
1–2 m	50.6 (31–71)	74.6 (36–116)*
2–3 m	64.2 (21–113)	104.5 (76–153)*
Sum	147.2 (87–210)	207.5 (140–248)**

[a] Mean number of contacts with shrubs on sampling pole, with range in parentheses (N = 10).
* Species differ at $P < 0.05$, Wilcoxon test.
** Species differ at $P < 0.01$, Wilcoxon test.

species principally responsible for the differing evergreen-to-deciduous ratio, was also significantly greater in Northern Waterthrush territories, as were IV's for *Alnus*. The remaining common deciduous species showed little interspecific difference, and territories of the species widely overlapped in all aspects of their forest cover.

A comparison of Boston Hollow with qualitatively studied sites in northern Connecticut showed similarities with habitats in steeply hilly regions, but differences with habitats in less hilly central and southern Connecticut. Typical Northern Waterthrush habitats in northern areas

TABLE 4
CHARACTERISTICS OF TREE COVER IN WATERTHRUSH TERRITORIES

Substrate	Louisiana Waterthrush	Northern Waterthrush
Betula lutea	89.5 (60.4–134.4)[a]	70.2 (14.6–104.9)
Acer rubrum	87.8 (55.3–138.9)	77.4 (32.1–173.6)
Alnus rugosa	10.2 (0–37.7)	23.8 (5.4–66.4)*
Tsuga canadensis	56.2 (0–109.0)	106.7 (8.3–164.1)*
Evergreen/deciduous	0.28 (0–0.71)	0.69 (0.04–1.46)**
Mean basal area (m/ha)	253 (176–319)	223 (196–281)
Trees/ha	666 (470–948)	913 (503–1238)*

[a] Mean importance value with range in parentheses (N = 10).
* Species differ at $P < 0.05$, Wilcoxon test.
** Species differ at $P < 0.01$, Wilcoxon test.

TABLE 5
MEASUREMENTS OF WATERTHRUSHES

Species	Wing length (cm)	Tail length (cm)	Mass (g)	Wing/$\sqrt[3]{\text{mass}}$	Tail/$\sqrt[3]{\text{mass}}$
Louisiana Waterthrush					
Male (N = 10)	8.2 ± 0.3[a]	5.3 ± 0.2	20.4 ± 1.2	3.0 ± 0.1	1.9 ± 0.1
Female (N = 7)	8.0 ± 0.2*	5.1 ± 0.1	20.9 ± 0.5	2.9 ± 0.1*	1.9 ± 0.1
Northern Waterthrush					
Male (N = 16)	7.5 ± 0.2	5.2 ± 0.2	16.1 ± 0.6	3.0 ± 0.1	2.1 ± 0.1
Female (N = 11)	7.3 ± 0.3*	5.1 ± 0.3	16.2 ± 0.7	2.9 ± 0.1	2.0 ± 0.1

[a] Mean ± SD.
* Sexes differ at $P < 0.05$, t-test.

were mixed deciduous-*Tsuga* swamps traversed by meandering streams (7 sites). Southern habitats were usually deciduous swamps (4 of 8 sites, one of which had few trees) or dense *Chamaecyparis* swamps (3 of 8 sites). Dense shrub cover was characteristic throughout. Moreover, breeding density was usually highest at mixed or coniferous sites.

The streamside habitats of Louisiana Waterthrushes in northern Connecticut were dominated by mixed deciduous-coniferous growth (8 of 9 sites), but in central and southern regions deciduous forest predominated (7 of 11 sites). The species also occurred along swampy streams (6 of 20 sites). Both species nested in close proximity, although uncommonly, throughout the state (5 of 26 sites).

Morphology.—During this study I measured 10 male and 7 female Louisiana Waterthrushes and 16 male and 11 female Northern Waterthrushes. Tests of wing and tail data suggested that females were slightly smaller than males in both species (Table 5). Females of both species (after egg laying) averaged slightly heavier than males, although not significantly so.

Male and female Louisiana Waterthrushes were significantly larger than male and female Northern Waterthrushes in mass (male: $t = 12.55$, df = 24, $P < 0.01$; female: $t = 14.76$, df = 13, $P < 0.01$) and wing chord (male: $t = 8.68$, df = 24, $P < 0.01$; female: $t = 6.40$, df = 16, $P < 0.01$), but not in tail length (male: $t = 0.17$, df = 24, $P > 0.05$; female: $t = 0.67$, df = 16, $P > 0.05$). Both sexes of the Northern Waterthrush also had greater relative tail length (male: $t = 4.76$, df = 23, $P < 0.01$; female: $t = 2.65$, df = 14, $P < 0.05$) than the respective sexes of the Louisiana Waterthrush, but similar relative wing length (male: $t = 1.90$, df = 23, $P > 0.05$; female: $t = 0.38$, df = 14, $P > 0.05$).

DISCUSSION

Four important differences exist in habitats used by the two waterthrush species at Boston Hollow. Northern Waterthrush territories were more densely vegetated than those of Louisiana Waterthrushes, as indicated by their greater shrub and tree density. They also had more evergreen cover by moss, shrubs, and trees, and possessed typical swamp characteristics such as abundant hummocks, ferns, and alders. In contrast, territories of Louisiana Waterthrushes had more fast-moving water. Despite these differences, the extent of intraspecific variation and species overlap in habitat use was great. Territories of Louisiana Waterthrushes ranged from deciduous-lined rocky streams to heavily coniferous, swampy streams, and those of Northern Waterthrushes ranged from largely coniferous swamps to swampy streams with deciduous cover.

In Connecticut, the habitat shift from north to south appeared largely attributable to a change in habitat availability. Conifers are common only in hilly, higher elevations of northern Connecticut, and deciduous forest dominates in less hilly southern regions (Dowhan and Craig 1976). However, *Chamaecyparis* swamps, which are present mostly in southeastern Connecticut, apparently were preferred by Northern Waterthrushes over the more abundant deciduous swamps. Anderson and Maxfield (1962) considered that deciduous swamps were only recently occupied by Northern Waterthrushes in Massachusetts. This also suggests that coniferous sites are preferred. In view of these observations, the habitats of Boston Hollow seem representative of the range of habitats used in Connecticut, but are more similar to sites used at higher elevations.

The major morphological differences between the two species were that Louisiana Waterthrushes were generally larger and relatively shorter tailed than Northern Waterthrushes. Longer tails theoretically can reduce stalling speed (Pennycuick 1975), and, when combined with lower body mass, this feature should enable Northern Waterthrushes to be more agile than Louisiana Waterthrushes, particularly in the dense foliage found in Northern Waterthrush habitats. This morphological difference may also be related to the greater amount of foraging in vegetation by Northern Waterthrushes compared to Louisiana Waterthrushes (Craig 1984).

The greater evergreen cover in Northern Waterthrush habitats compared to Louisiana Waterthrush habitats may be related to prevailing conditions over the ranges of the species, with conifers predominating in the largely boreal range of Northern Waterthrushes, and deciduous growth predominating over the southeastern piedmont range of Louisiana Waterthrushes. Each species might use such vegetation features as cues in selecting breeding sites (Morse 1980), and hence characteristic habitat

associations could persist even where suitable alternative habitats are common.

I cannot explain why Louisiana Waterthrushes seem to prefer streams or why Northern Waterthrushes seem to prefer slow-moving water. Characteristics of the water may simply reflect preferred vegetation features, or they may be related to foraging specializations.

In light of the demonstrated wide overlap in habitat use and my previous findings of considerable overlap in foraging behavior (Craig 1984), the two species appear ecologically similar, at least in Connecticut. They coexist, however, without aggression (Craig 1984), indicating that interference competition is not occurring. The notion that interspecific competition limits ecological similarity, although not without merit (Karr 1983), has sometimes led to alternative explanations being ignored (Wiens 1983).

Evidence of little interspecific competition also comes from recent range expansions by both species. The Northern Waterthrush was unknown as a Connecticut breeder into the early 20th century (Sage et al. 1913; but see Bent 1953 for a 1908 report from coastal Rhode Island), but became well established in Connecticut (Kuerzi and Kuerzi 1934) and Massachusetts (Bagg and Eliot 1937) by the 1930s. Similarly, the Louisiana Waterthrush was formerly common primarily in southern Connecticut (Sage et al. 1913) but since about 1920 has increased in Massachusetts (Bagg and Eliot 1937) and is now found to northern New England (Tingley 1983).

Lack of aggression between similar species has sometimes been attributed to past competition having caused necessary niche partitioning (Noon 1981). The roughly 50 years that the species have been in frequent contact, however, seems a short time for refinement of such niche shifts. Yet, I have observed no interspecific aggression, appreciable behavioral difference (Craig 1984), or consistent habitat segregation by the two species. I therefore propose that habitat use by the Louisiana and Northern waterthrushes can best be explained in terms of independent evolutionary histories and individual ecological requirements.

SUMMARY

Habitat use by the Louisiana (*Seiurus motacilla*) and Northern (*S. noveboracensis*) waterthrushes was studied at Boston Hollow in northeastern Connecticut. Territories of Northern Waterthrushes had significantly greater shrub and tree density, more evergreen cover by moss, shrubs, and trees, and more swamp related features such as hummocks, ferns, and alders, but less fast-moving water than those of Louisiana Waterthrushes. Despite statistical differences, however, both species occupied a wide range of habitats and overlapped considerably in habitat use. The habitats at Boston Hollow seemed representative of the range

of habitats used throughout Connecticut, but were more similar to those used at higher elevations. Both species coexisted without aggression even though they overlapped in habitat use and in territorial boundaries. Observed patterns of habitat use appear best explained in terms of independently evolved ecological requirements of each species.

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GENERAL NOTES

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An ecological comparison of the avifaunas of Grenada and Tobago, West Indies.—Low numbers of species and the absence of many neotropical families are characteristics of the bird faunas of West Indian islands. Although the West Indian avifauna is partly a subset of both the Neotropical and Nearctic avifaunas, it does have distinctive elements and has been described as a separate avifauna (Bond, Proc. Acad. Nat. Sci. Phila. 115:79–98, 1963; Lack, Island Biology, Univ. California Press, Berkeley, California, 1976). The southeastern boundary of this avifaunal region lies between the islands of Grenada and Tobago. The difference in the avifaunas of these adjacent (120 km) islands is so dramatic that Lack (1976) proposed calling this boundary "Bond's Line" in honor of James Bond, the avian zoogeographer of the West Indies. The avifauna of Tobago is South American, while that of Grenada is primarily West Indian with a strong South American element. Common South American families that occur on Tobago, but are absent from Grenada and the rest of the Lesser Antilles, include Nyctibiidae, Trogonidae, Momotidae, Galbulidae, Dendrocolaptidae, Furnariidae, Formicariidae, Cotingidae, and Pipridae. The most striking difference between the two islands, however, is the presence of twice as many species of land birds on Tobago as on Grenada (70 vs 35; Lack 1976). Eighteen terrestrial species are common to both islands.

Despite the differences in avifaunas, the islands of Grenada and Tobago are similar in size (310 km and 300 km respectively), climate, cultivated crops, area under cultivation, and recent disturbance by hurricanes (Grenada, Hurricane Janet 1955; Tobago, Hurricane Flora 1963). Maximum elevations are less on Tobago than Grenada (580 m and 840 m respectively). Also, Tobago's forests are floristically richer than those of Grenada (Beard, Ecol. Monogr. 14:135–163, 1944; Beard, The Natural Vegetation of the Windward and Leeward Islands, Clarendon Press. Oxford, England, 1949). Both islands are located about 130 km from South America, although Tobago is only 35–40 km from the island of Trinidad. Tobago is a continental island, and was connected to the mainland until early in the Pleistocene (Lack 1976). Grenada is an oceanic island that arose as a volcano from the sea. Here, I report a preliminary survey of both habitat use and frequency of occurrence of birds on the two islands and investigate some aspects of ecological release.

From the earlier literature (e.g., Crowell, Ecology 42:75–88, 1962; Keast, Biotropica 2: 61–75, 1970; Diamond, Proc. Natl. Acad. Sci. 67:529–536, 1971; Cox and Ricklefs, Oikos 28:113–122, 1977), I predicted that the relatively depauperate Grenadian avifauna would show greater ecological release (e.g., a wider variety of habitats used and higher frequencies of occurrences within habitats) than the larger avifauna of Tobago. In addition, I hypothesized that those species that have successfully colonized other islands in the Lesser Antilles would show more ecological release than species from South America restricted to only Grenada and Tobago.

Methods.—Bird communities in nine different habitats—grassland, scrub, young secondary forest, old secondary forest, mature lowland forest, cloud forest, savanna, mangrove forest, and residential parklands—were censused on both Grenada and Tobago. Foliage height profiles were made for all habitats on both islands except residential parklands. I was able to match most of my habitats with those studied in Trinidad, Jamaica, and St. Lucia by Cox and Ricklefs (1977) on the basis of foliage height profiles (using their technique) and their published descriptions. I also tried to study sites with matching rainfall and altitude on the two islands. With the exception of mature lowland forest (see below), the habitat types appeared to be roughly equivalent in size, and were contiguous with other habitats of

similar foliage profiles. The habitat types and localities selected for study sites on Grenada and Tobago are described below:

(1) *Secondary grassland.*—Dry pasturelands containing a mixture of predominantly perennial grasses, some herbs, and an occasional woody shrub were censused at Calliste (SW Grenada) and near Crown Point Airport (W Tobago). Both sites were grazed, and 99% of the vegetation was below 3 m covering an area of about 150 ha.

(2) *Secondary scrub.*—Old farmland with shrubs, saplings, and scattered patches of herbs were censused near the golf course, Grenada, and near Mt. Irvine, Tobago. Both sites were located in hilly areas, with 90% of the plant foliage below 9 m covering an area of about 250–300 ha.

(3) *Young secondary forest.*—The young forest on both islands had an open canopy at approximately 6 m with a few individual trees reaching 10 m. The understory contained a dense growth of shrubs and scattered patches of herbs. Both sites covering about 175–350 ha were located on hilly locales: Halifax Harbor, Grenada, and Grafton Estate, Tobago (both approximately 150 m above sea level).

(4) *Old secondary forest.*—This forest contained a closed canopy 18–22 m high, with occasional trees reaching 24 m. The open understory contained only a few scattered shrubs and a few herbs. The secondary forest sites were located at Mt. Granby, Grenada, and southwest of Kings Bay, Tobago, both on steep slopes and covering areas of about 125–225 ha.

(5) *Mature lowland forest.*—This is probably the rarest habitat on both islands because of recent hurricanes and agricultural clearing. Both sites had a closed canopy at a height of 20–25 m, with an occasional tree exceeding 26 m. Except for scattered second growth in tree falls, the understory was open and consisted of small tree seedlings. Remnants of lowland moist forest were found on the slopes of Morne Delice at an altitude of 300 m on Grenada and on slopes at 200 m at Kings Bay, Tobago. The Grenada site of about 75 ha was completely surrounded by cultivated land and young forest, whereas the Tobago site was larger (about 150 ha) and surrounded by old secondary forest.

(6) *Cloud forest.*—Both sites were located on ridges at 590 m at Grand Etang, Grenada, and at 550 m in the forest reserve just north of Roxborough, Tobago. The trees were covered with epiphytes, and scattered palms were present in the understory and lower forest canopy. The 15–18 m canopy was closed on Grenada, but partially open (25–40%) on Tobago. Cloud forests covered the higher regions on both islands covering about 500–700 ha.

(7) *Savanna.*—Both sites were at sea level in the drier parts of the islands (Calliste, Grenada; Crown Point, Tobago). Both were heavily grazed with scattered trees and shrubs, mostly <4 m high in an area of about 150–250 ha.

(8) *Mangrove forest.*—Red (*Rhizophora mangle*) and black mangroves (*Avicennia nitida*) with open canopies at a height of about 8–10 m dominated the sample sites at Levera Beach, Grenada, and Bucco, Tobago. On both islands the two habitats were very limited in size (about 50–75 ha).

(9) *Residential parklands.*—This habitat consisted of extensive lawn areas with ornamental herbs, shrubs, and trees, surrounding private homes or hotels at Westerhall Point, Grenada, and at Mt. Irvine, Tobago, covering about 250–400 ha.

Vegetation density profiles of all habitats except residential parkland were made directly from measurements of the basal area per hectare of plant stems by dividing the area into fractions associated with foliage at different heights. A nested quadrat method, in which woody and herbaceous plants with various circumferences at breast height were counted on plots of different sizes, was used to sample representative vegetation in each habitat. The basal area per ha for trees in each circumference class was allocated to estimated height zones according to the percent of the canopy estimated in each height zone for a specific

sample tree. The height profile is thus based on basal area. For details of this technique see Cox and Ricklefs (1977).

I calculated similarity coefficients using the following equation (after Cox and Ricklefs, 1977):

$$C = \frac{2W}{a + b}$$

Similarity coefficients (C) were computed from the distribution among the 9 height zones of basal area per hectare. W indicates the sum, over the various height zones, of the smaller of the basal area component values (m^2 ha^{-1}) for corresponding heights in the compared habitats, and a and b represent the basal area totals for the two habitats. The coefficient varies from 0 to 1, with 1 representing complete overlap of height profiles.

Field work was conducted on Grenada from 16 to 25 November 1981 and on Tobago from 1 to 22 December 1981. Both islands were sampled during the wet season after the peak of breeding, although some species were still nesting. I used a census technique developed by Blondel et al. (Alauda 38:55–71, 1970), which was used in the West Indies by Cox and Ricklefs (1977). The technique gave a high correlation with other counts based on number of individuals seen per hour on the island of St. Lucia. On Grenada, I found that the technique gave a high correlation with both mist-net results and number of individuals seen per hour in residential areas, savanna, and scrub habitats (Wunderle, unpubl. data). The census technique consisted of observations at 10 points: all species (except raptors, migrants, and nocturnal species) heard or seen were recorded during 20-min periods at each point (see Appendixes 1 and 2). All observations were made in the morning, and all 10 observation points within a habitat were made on the same day. Observations were stopped only during heavy rains. The observation points within a habitat were at least 100 m from each other, and it is unlikely that individuals were recorded at more than one point. From the 10 observation periods per habitat, I determined the number of species per habitat, the number of times a species was present in each of the 10 observation periods within a habitat (designated as occurrences per habitat), and the number of times a species was present in each of the 10 periods, given that it occurred in at least one of the 10 periods (designated as the number of occurrences per habitat occupied). The resulting index of abundance calculated from these observations is valuable for comparing the same species within the same habitat on different islands. Comparisons between different species or between different habitats represent differences in conspicuousness as well as abundance.

Results.—Many of the 9 habitats found on both Grenada and Tobago had closely matching vegetation profiles (Table 1). The basal areas and the distribution of foliage in the different height zones fall within the range of corresponding Caribbean habitats sampled by Cox and Ricklefs (1977). For the same habitats on the two islands, I found high similarity coefficients for the mature lowland forest (0.86), savanna (0.85), and grasslands (0.85). Less similarity was found between the scrub (0.69), mangrove forest (0.69), cloud forest (0.57), old secondary forest (0.54), and young secondary forest (0.52). The mean coefficient of similarity for the same habitats on Grenada and Tobago was 0.70. These findings indicate that the corresponding habitats on the two islands were at least as similar in basal area and foliage profiles as the most similar habitats on the same island. In addition, the habitat matchings were based on features other than foliage profiles that may be even more important to the birds.

Thirty species of birds were found on Grenada compared with 53 on Tobago, representing 88.2% and 77.9%, respectively, of the known terrestrial nonraptorial species for the two islands (Table 2). The Grenada findings are comparable to those of Cox and Ricklefs (1977) for St. Lucia (N = 34 species observed, 85% of known species in counts). The Tobago results fall between those obtained by the same authors for Trinidad (N = 108, 58%) and Jamaica (N = 55, 86%).

TABLE 1

BASAL AREA PER HECTARE AND PERCENTAGES OF TOTAL BASAL AREA ASSOCIATED WITH MAJOR FOLIAGE HEIGHT ZONES FOR WOODY AND HERBACEOUS PLANTS SAMPLED ON GRENADA AND TOBAGO

Community	Basal area (m^2ha^{-1})		Basal area % association with successive foliage height zones (m)			
	Woody plants	Herbaceous plants	0–3	3–9	9–23	23–45
Secondary grassland						
Grenada	0.1	45.8	100	0	0	0
Tobago	0.0	62.4	100	0	0	0
Secondary scrub						
Grenada	28.9	13.5	75.9	23.3	0.8	0
Tobago	20.7	16.9	66.1	31.3	2.6	0
Young secondary forest						
Grenada	25.7	1.7	36.4	41.6	23.0	0
Tobago	34.3	1.2	37.7	47.9	14.4	0
Old secondary forest						
Grenada	41.1	3.2	10.0	16.4	65.2	8.4
Tobago	43.9	0.1	0.2	13.1	76.5	10.2
Mature lowland forest						
Grenada	81.3	0	2.9	20.9	49.1	27.1
Tobago	87.2	0	1.1	2.7	66.6	29.6
Cloud forest						
Grenada	55.8	8.6	15.0	31.2	50.7	3.1
Tobago	52.8	11.1	18.1	7.8	74.1	0
Savanna						
Grenada	4.6	52.1	97.6	2.4	0	0
Tobago	3.3	49.7	99.9	0.1	0	0
Mangrove forest						
Grenada	27.6	0	7.0	57.4	35.6	0
Tobago	24.7	0	4.7	72.4	22.9	0

Besides a lower number of total species, Grenada also had a significantly (Mann-Whitney U Test, $U = 65$, $P < 0.05$) lower average number of species per habitat when compared with Tobago (15.6 vs 21.4). On Tobago, the number of species per habitat ranged from 10 in secondary grassland to 30 in secondary scrub. Variability was less on Grenada, ranging from 11 species in secondary grassland to 20 species in secondary scrub and savanna. These differences are consistent with those for other Caribbean islands (Cox and Ricklefs, 1977).

The total number of observations was 758 on Grenada and 916 on Tobago. The variation in these values fell within the range (621–934) found by Cox and Ricklefs (1977), despite the fact that all my observations were made past the peak of breeding at a time when

TABLE 2

SUMMARY OF STANDARDIZED OBSERVATIONS OF BIRDS IN NINE HABITATS ON GRENADA AND TOBAGO[a]

	Grenada	Tobago
Terrestrial species in fauna (excluding owls)	34	68
Terrestrial species in counts	30	53
Number of species/total occurrences of all species		
Secondary grassland	11/61	10/55
Secondary scrub	20/101	30/150
Young secondary forest	19/112	28/137
Old secondary forest	14/79	22/99
Mature lowland forest	11/55	21/93
Cloud forest	15/78	25/103
Savanna	20/127	19/106
Mangrove forest	12/49	18/65
Residential	18/96	20/108
Total all habitats	140/758	193/916
Mean	15.5/84.2	21.4/101.8
Mean habitats per species	4.63	3.63
Mean occurrence per habitat occupied	5.36	4.71
Mean occurrences per species	24.80	17.22
Relationship of number of species to total occurrences		
Correlation coefficient	0.95[b]	0.91[b]
Slope	0.13	0.18
Intercept	4.29	3.29

[a] Based on 10, 20-min observation periods in each habitat.
[b] $P < 0.01$.

conspicuousness might be low. Variation in these values represent differences in conspicuousness or abundance.

On both islands, a positive correlation was found between the number of species in a habitat and number of occurrences. A positive correlation was also found between the number of habitats and average number of occurrences per habitat on both islands (Table 2). This indicates that species that are widespread on an island tend to be abundant in the habitats they occupy (cf. Ricklefs and Cox, Am. Nat. 112:875–895, 1978). Locally distributed species, however, are not necessarily rare in the habitats they occupy.

Associated with Grenada's lower number of species was an increase in the mean number of habitats used by each species, an increase in mean occurrences per habitat occupied, and an increase in mean occurrences per species (Table 2). These findings are consistent with previous studies (e.g., Crowell 1962, MacArthur et al., Am. Nat. 100:319–332, 1976; Cox and Ricklefs 1977) that showed that bird populations respond to smaller number of bird species both by expanding through different habitats and increasing local population density.

A better understanding of ecological release might be obtained by examining both number of habitats and number of occurrences for individual species and groups of species on the two islands. To examine the possibility that species common to both islands might show greater ecological release on species-poor Grenada, I made the following comparisons for

16 of the 18 species found on both islands: the mean number of habitats per species (4.75 ± 2.44 SD Grenada; 4.58 ± 2.10 Tobago), mean number of occurrences per species (26.94 ± 19.85 Grenada; 28.14 ± 19.51 Tobago), and mean occurrences per habitat occupied (5.12 ± 2.18 Grenada; 5.18 ± 2.34 Tobago). No significant differences were found between these parameters in the species common to the two islands, supporting the statement of Ricklefs and Cox (1977:889), regarding island colonists, that "the degree of ecological release appears to be unrelated to the number of co-occuring species on islands." Thus, while the total avifauna of Grenada appears to show characteristics of ecological release when compared with Tobago, species common to both islands do not demonstrate ecological release.

Do species that have colonized other islands in the Lesser Antilles (LA) show more ecological release than species from South America (SA) restricted to only Grenada or Tobago in the Caribbean? To answer this question, I compared the ecological release parameters of species belonging to these two groups. Lack (1976:390) lists six SA species that have colonized only Grenada in the Lesser Antilles. He also suggested that *Leptotila wellsi* is in the same superspecies as *L. verreauxi* of South America, which increases the SA list to seven on Grenada. The five SA species (*Leptotila wellsi, Chaetura cinereiventris, Glaucis hirsuta, Sporophila nigricollis, Volatinia jacarina*) that I observed on Grenada had a mean number of habitats per species of 2.8 ± 1.48 vs 5.0 ± 2.31 for 25 L.A. species on Grenada (one-tailed Mann-Whitney U test, $U = 2.27$, $P < 0.01$). A suggestive, but not significant, difference was found between SA and LA groups on Grenada in the average number of occurrences per species (14.0 ± 13.98 vs 26.9 ± 19.10; $U = 1.530$, $P < 0.10$). No significant difference (one-tailed Mann-Whitney U test, $U = 0.498$, $P > 0.10$) was found between SA and LA groups in the average number of occurrences per habitat occupied (4.16 ± 2.07 vs 4.98 ± 2.29).

On Tobago, I observed 14 species common to the Lesser Antilles and 35 species restricted to Tobago, Trinidad, and South America. Significant differences between SA and LA groups were found in the mean number of habitats per species (3.14 ± 5.81 vs 4.57 ± 4.42; $U = 1.94$, $P < 0.05$), mean number of occurrences per species (13.57 ± 16.11 vs 28.14 ± 1.95; $U = 3.13$, $P < 0.01$), and mean occurrences per habitat occupied (3.32 ± 1.89 vs 5.18 ± 2.34; $U = 2.91$, $P < 0.005$). Data from Tobago, as well as those from Grenada, suggest that the successful Caribbean colonizers (LA species) occupy more habitats and maintain higher population densities than the SA species restricted to Grenada or Tobago. As these census results are also a measure of relative conspicuousness, it is also possible that the LA species are more conspicuous or are found in habitats where they might be more apparent than the SA species.

Which avian communities on Grenada are most and least similar to communities on Tobago? To answer this question, I calculated bird community similarity coefficients for each of the nine habitats, comparing one habitat with the corresponding habitat on the other island. The most similar bird communities of the two islands were grassland (0.50), savanna (0.46), mangrove forest (0.45), and residential parkland (0.44). The least similar were cloud forest (0.21), young secondary forest (0.22), old secondary forest (0.22), mature lowland forest (0.28), and scrub (0.31). These findings are consistent with Lack's (1976) observations that the species common to the two islands were abundant in the human-disturbed sites of Tobago, but not in the woodland areas. There was a significant correlation ($r = 0.74$, $P < 0.05$) between the bird-community similarity coefficients and vegetation-community similarity coefficients for the respective habitats on the two islands.

It is possible to investigate the similarities of communities in more detail by examining the species composition within those communities. On Tobago, the LA species are most abundant in open human-disturbed sites, with scrub sites having the most LA species (N = 13) and cloud forest having the least (N = 3). The SA species restricted to Tobago were

most common in the forested habitats (young secondary forest, N = 18; old secondary forest, N = 16; mature lowland forest, N = 15; cloud forest, N = 18), and least common in the open disturbed sites (residential, N = 8; savanna, N = 10; scrub, N = 13, grassland, N = 2). On Grenada, the SA species with a limited Caribbean distribution (Grenada only) are most abundant in open areas (scrub, N = 3; young secondary forest, N = 3; grassland, N = 2; savanna, N = 2). The presence of the geographically widespread island species in human-disturbed habitats is consistent with previous observations (see review by MacArthur and Wilson, The Theory of Island Biogeography, Princeton Univ. Press, Princeton, New Jersey, 1967).

Discussion.—Despite the two-fold difference in number of species between the two islands, there was no difference in parameters of ecological release (number of habitats or number of occurrences) for the 16 species observed on both islands. This suggests that the carrying capacities for these species are similar on the two islands, even though the number of potential competitors is quite different. Also, high levels of gene flow between the island populations or a short history in isolation might explain why species common to both islands have similar habitat preferences (and occurrence levels) and fail to show signs of ecological release. Hence the difference in ecological release of the avifaunas of the two islands is attributable largely to differences between the SA species and the LA species. On Tobago, the SA species were most common in the forested regions and showed the least ecological release, while on Grenada the SA species were most abundant in open or disturbed sites. The LA species on Tobago showed the most ecological release and were most abundant in open or human-disturbed sites.

These findings suggest that "ecological release" within the Caribbean avifauna is an artifact of the species composition rather than actual ecological release by the individual species. While the total avifauna might appear to show ecological release, none or few of the individual species actually change their habitat breadth or population density. Instead, species with low density populations and narrow habitat preferences disappear, leaving only those species with high density populations and wide habitat preferences. For example, as one proceeds from larger to smaller islands or from continental to more distant islands, one would expect the number of montane rainforest species (with narrow habitat tolerances) to decrease, leaving an avifauna with only generalist species having wide habitat tolerances. Montane rainforest species might be absent from many Caribbean islands for several reasons. For instance, Pregill and Olson (Annu. Rev. Ecol. Syst. 12:75–98, 1981) provide evidence suggesting that arid xerophitic habitats were the predominate habitat of the West Indies during the late Pleistocene. Thus, montane rainforests were much reduced in area and, therefore, more difficult to colonize and less likely to maintain viable populations. This, together with the fact that rainforest species are poor dispersers, would explain why rainforest species are absent from smaller and more distant islands.

Evidence from the fossil record indicates that environmental conditions in the West Indies during the last Pleistocene glaciation differed from those of the present by the predominance of arid habitats (Pregill and Olson 1981). Xeric scrub vegetation was more abundant on all low lying West Indian islands at that time than it is now. The Lesser Antillean avifauna consists mainly of xeric scrub-adapted species that have invaded mesic habitats (Terborgh et al., Auk 95:59–72, 1978), probably as a result of the earlier climatic conditions (Pregill and Olson 1981). In my study, the highest mean avian community similarity coefficient occurred in secondary (xeric) scrub on Grenada and savanna on Tobago, which is consistent with the paleoclimatic evidence. In other words, on Grenada and Tobago the habitats having the avifauna most similar to the remaining habitats are the drier habitats. As neotropical forest birds have relatively low dispersal abilities, the mesic forests may have been historically depauperate and hence available for colonization by island species from nearby xeric scrub areas.

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Appendix 1

Habitat Occurrences of Birds on Grenada[a]

Species	Habitats								
	G[b]	SC	YSF	OSF	ML	CF	SA	MA	R
Columba squamosa	—	—	2	—	6	6	—	1	1
Zenaida auriculata	4	3	7	—	—	—	6	—	4
Z. aurita	—	—	—	—	2	—	2	3	2
Columbina passerina	6	7	7	—	—	—	8	—	8
Leptotila wellsi	—	2	5	—	—	—	—	—	—
Geotrygon montana	—	—	—	—	—	3	—	—	—
Coccyzus minor	—	4	4	2	1	2	1	—	3
Crotophaga ani	2	1	—	—	—	—	6	—	—
Chaetura cinereiventris	—	—	2	—	—	—	—	—	—
Glaucis hirsuta	—	—	7	10	10	10	—	—	1
Eulampis holosericeus	—	—	1	2	—	1	—	—	—
Orthorhyncus cristatus	—	9	6	10	7	10	9	3	10
Tyrannus dominicensis	4	4	6	3	1	1	5	3	3
Myiarchus tyrannulus	—	4	9	4	—	4	6	4	3
Elaenia flavogaster	—	6	4	—	—	—	10	—	1
E. martinica	—	—	—	1	—	2	—	—	—
Progne subis	1	—	—	—	—	—	2	—	—
Troglodytes aedon	—	1	5	—	—	—	7	—	10
Mimus gilvus	5	10	9	—	—	—	10	3	10
Turdus nudigenis	—	8	8	2	1	—	7	7	8
T. fumigatus	—	—	—	10	—	6	—	—	—
Vireo altiloquus	—	—	—	8	9	8	—	3	—
Coereba flaveola	—	9	10	10	10	9	8	10	10
Tangara cucullata	—	7	4	10	5	8	—	3	—
Molothrus bonariensis	5	—	—	—	—	—	6	—	4
Quiscalus lugubris	6	9	9	2	1	1	10	7	6
Volatinia jacarina	7	1	—	—	—	—	4	—	—
Sporophila nigricollis	4	2	—	—	—	—	5	—	—
Loxigilla noctis	—	7	7	5	—	4	5	2	10
Tiaris bicolor	9	6	—	—	—	—	10	—	3

[a] Each number represents the number of 20-min observation periods in which a species was present during 10 observation periods in each habitat.

[b] Acronyms for habitats are as follows: G = Secondary grassland, SC = Secondary scrub, YSF = Young secondary forest, OSF = Old secondary forest, ML = Mature lowland forest, CF = Cloud forest, SA = Savanna, MA = Mangrove forest, R = Residential.

Appendix 2

Habitat Occurrences of Birds on Tobago[a]

Species	Habitats								
	G[b]	SC	YSF	OSF	ML	CF	SA	MA	R
Columba cayennensis	—	—	—	—	2	5	—	—	—
Zenaida auriculata	3	7	1	—	—	—	8	4	10
Columbina talpacoti	4	4	1	—	—	—	5	—	2
Leptotila verreauxi	—	7	9	7	9	2	7	5	2
Amazona amazonica	—	—	—	3	—	10	—	—	—
Coccyzus minor	—	—	—	—	—	—	—	1	—
Crotophaga ani	5	2	—	—	—	—	3	1	3
Chaetura brachyura	—	1	5	—	—	—	—	—	—
Glaucis hirsuta	—	—	—	8	9	10	—	—	—
Florisuga mellivora	—	—	—	—	—	4	—	—	—
Anthracothroax nigricollis	—	3	—	—	—	—	—	—	5
Chrysolampis mosquitus	—	2	—	—	—	—	1	2	—
Amazilia tobaci	—	9	9	9	10	10	7	3	3
Trogon collaris	—	—	—	—	—	3	—	—	—
Momotus momota	—	—	5	1	3	4	—	—	—
Galbula ruficauda	—	—	4	—	—	4	—	—	—
Melanerpes rubricapillus	—	4	7	1	2	—	—	3	6
Veniliornis kirkii	—	—	—	—	2	—	—	—	—
Dendrocincla fuliginosa	—	—	—	—	—	1	—	—	—
Sittasomus griseicapillus	—	—	3	—	1	—	—	—	—
Xiphorhynchus guttatus	—	—	8	7	4	3	—	—	—
Synallaxis cinnamomea	—	—	4	1	—	4	—	—	—
Thamnophilus doliatus	—	10	9	8	7	9	8	3	5
Dysithamnus mentalis	—	—	—	—	—	1	—	—	—
Formicivora grisea	—	6	8	7	6	—	8	1	—
Pachyramphus polychopterus	—	2	—	—	—	—	—	—	—
Chiroxiphia pareola	—	—	2	6	3	4	—	—	—
Tyrannus melancholicus	7	4	2	2	2	1	1	1	3
T. dominicensis	1	3	—	—	—	—	—	—	—
Myiodynastes maculatus	—	—	—	—	—	1	—	—	—
Myiarchus tyrannulus	—	2	1	—	1	—	—	5	—
M. venezuelensis	—	—	—	—	—	—	1	—	—
Cnemotriccus fuscatus	—	—	1	—	—	—	—	—	—
Tolmomyias flaviventris	—	—	10	4	6	3	—	—	—
Elaenia flavogaster	—	9	5	2	1	2	7	—	8
Mionectes oleagineus	—	—	—	2	—	—	—	—	—
Thryothorus rutilus	—	—	5	2	1	2	—	—	—
Troglodytes aedon	—	7	6	5	—	—	—	—	3
Mimus gilvus	6	10	2	—	—	—	10	2	10
Platycichla flavipes	—	—	—	—	—	3	—	—	—
Turdus nudigenis	—	6	4	2	3	—	3	8	8
Vireo chivi	—	—	—	—	1	—	—	—	—
Hylophilus flavipes	—	5	4	4	—	—	5	4	—

Appendix 2
Continued

Species	Habitats								
	G[b]	SC	YSF	OSF	ML	CF	SA	MA	R
Molothrus bonariensis	—	2	—	—	—	—	—	—	—
Scaphidura oryzivora	—	2	—	—	—	—	—	—	—
Psarocolius decumanus	—	5	3	2	4	5	—	2	1
Quiscalus lugubris	6	1	—	—	—	—	4	9	6
Sturnella militaris	3	—	—	—	—	—	—	—	—
Coereba flaveola	—	10	10	10	10	10	9	10	10
Thraupis episcopus	—	6	4	4	6	—	2	2	5
Tachyphonus rufus	—	2	—	—	—	1	—	—	—
Volatinia jacarina	10	9	3	—	—	—	9	—	8
Tiaris bicolor	10	5	—	—	—	—	8	—	10

[b] For acronyms and explanation see footnote of Appendix 1.

Wilson Bull., 97(3), 1985, pp. 365–366

Seasonal distribution of subadult Bald Eagles in three Minnesota habitats.—Although the biology of breeding and wintering Bald Eagles (*Haliaeetus leucocephalus*) has been much studied, little is known of the biology of subadults during the breeding season. In this note we describe seasonal changes in abundance of subadult Bald Eagles in three types of shoreline habitat.

The study was conducted on a 1500 km² area in the center of the Chippewa National Forest (CNF) in north central Minnesota. The area is mostly glacial outwash and lacustrine plain and has numerous rivers, creeks, and lakes. We observed segments of shoreline from fixed-wing aircraft at approximately weekly intervals (6–10 days) from 21 March to 30 September in 1977 and 1978. We flew at 30–60 m above the ground and recorded the plumage and location of all eagles observed. The area surveyed on each flight included approximately 39 km of river shoreline (Mississippi and Leech Lake rivers), 26 km of small (1–210 ha) lake shoreline, and 128 km of large (370–44,280 ha) lake shoreline. In this note, subadult eagles refers to those with off-white to brown heads and tails (Southern's plumages A–E, Jack-Pine Warbler 45:70–80, 1967). Counts are reported as means ± 1 SE.

We recorded 1159 observations of subadult Bald Eagles on 56 aerial surveys. The mean number of birds observed per flight was 20.7 ± 1.7 (range 0–62). Few birds were observed in March, September, and October; peak counts occurred in mid-April, and intermediate numbers were seen in May–August (Fig. 1). The mean number of subadults per flight in September–October was lower than for any other month except March. We observed 860 birds on large lakes, 83 on small lakes, and 216 on rivers. These frequencies differed from the numbers expected (769, 156, and 234, respectively) based on the relative amounts of the three types of shoreline surveyed ($\chi^2 = 46$, df = 2, $P < 0.001$).

Most lakes in the study area were ice-covered until early or mid-May, and eagles exhibited greater use of rivers in March through May than during the balance of the year ($\chi^2 = 115$, df = 1, $P < 0.001$) (Fig. 1). Eagles observed on lakes before ice-out often were near fish discarded by ice fishermen.

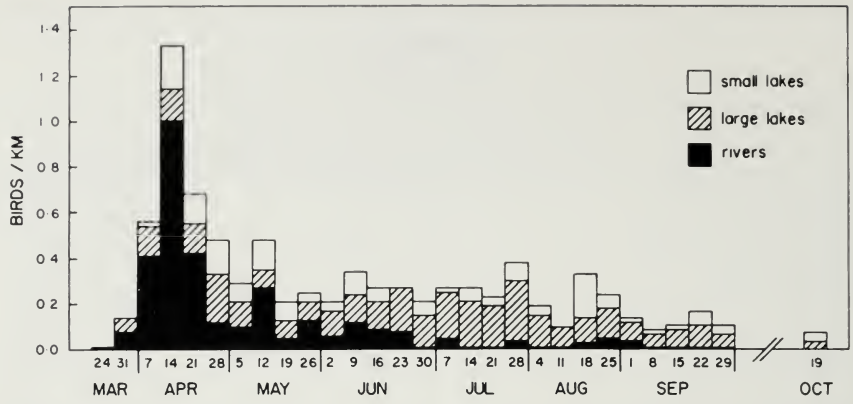

FIG. 1. Subadult Bald Eagles observed/km of shoreline during aerial surveys, Chippewa National Forest, Minnesota, 1977–78.

We interpret the mid-April peak as a migratory wave. The decline that followed may be due partly to continued northward migration and partly to shifts to small creeks not covered by our surveys. Several groups of eagles were observed on such creeks and may have been attracted by spawning suckers (*Catostomus commersoni, Moxotoma macrolepidotum*), which are important Bald Eagle foods in the Spring (Dunstan and Harper, J. Wildl. Manage. 39: 140–143, 1975). We suggest that as the number of spawning fish declines, eagles begin to search for food, and tend to move to large lakes where more abundant food supplies may exist during summer and autumn. Because riparian areas are being developed rapidly for housing and recreation, inventory of existing undeveloped shoreline and the acquisition of habitat or conservation easements by responsible agencies seems appropriate.

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Skua predation on penguin eggs: the influence of egg quality and location.—Versatile predatory birds such as the *Catharacta* skuas (Murphy, Oceanic Birds of South America, American Museum of Natural History, New York, New York, 1936) face two potentially conflicting requirements. On the one hand they must be able to assess prey profitability with

minimum expenditure of time or energy (Hughes, Am. Nat. 113:209–221, 1979). On the other hand they must regularly sample potential sources of prey so that new sources do not go unexploited. Such sampling is often, and I believe reasonably, invoked to explain deviations by birds from the predictions of short-term maximization of energy gain (e.g., Krebs, pp. 23–63 *in* Behavioural Ecology, J. R. Krebs and N. B. Davies, eds., Blackwell, Oxford, England, 1978). The present study of Subantarctic Skuas (*Catharacta antarctica*) shows that they possess the ability to discriminate items of different profitability. They nevertheless do sometimes take prey (broken egg shells) that in all normal circumstances have zero value. I attribute this to the need to sample the environment continually in order to discover new prey sources.

Throughout the Antarctic (Jouventin and Guillotin, Terre et Vie 33:109–127, 1979) and Subantarctic (Stonehouse, F.I.D.S. Sci. Repts. No. 14:1–25, 1956) penguin colonies are harassed by *Catharacta* skuas. At Marion Island (46°53′S, 37°52′E) in the Southern Ocean, Subantarctic Skuas are major egg predators of Macaroni Penguins (*Eudyptes chrysolophus*), which nest in colonies of up to about 200,000 pairs. Skuas continually patrol the penguin colonies, and, whenever an egg is exposed, snatch it up and then usually carry it beyond the colony to eat. As a result, the land bordering the colony is littered with discarded penguin egg shells and eggs with holes. Yet the skuas do not continually investigate such eggs. This suggests that the skuas use the location of the egg, within the colony vs without, as a cue on which to base the decision whether or not to approach.

To test this, eggs were placed at various distances from the penguin colony and among the nesting penguins. This preliminary experiment failed because penguins kicked aside, attempted to incubate, or otherwise molested test eggs placed within the colony. Accordingly, two experiments were carried out that showed that skuas used both the location (Experiment one) and condition (Experiment two) of the potential egg prey as cues. The experiments were completed between 27 December 1983 and 12 January 1984, at the very end of the Macaroni Penguin incubation period.

In Experiment one, five Macaroni Penguin eggs were placed in each of the following four locations: (a) on the ground and not obscured by grass, 20 m from the edge of the penguin colony, (b) as (a) but 50 m from the edge of the penguin colony, (c) in a Southern Giant Petrel (*Macronectes giganteus*) nest that was transferred, by lifting the entire tussock grass mat that constituted the nest, from the petrel colony to a position 5 m from a (b) egg, and (d) in a Southern Giant Petrel nest that was unoccupied but still in situ within the petrel colony and also about 50 m from the edge of the penguin colony. The test eggs were predated penguin eggs with small holes such that, when the eggs were placed hole downward, they appeared intact. Macaroni Penguin eggs resemble in size, color, and shape the eggs of the Southern Giant Petrel. The eggs were filled with earth so that they weighed approximately the same as whole eggs. The eggs were checked 1, 2, and 6 h after placement. I then determined which eggs were undisturbed and which had been moved or broken open by skuas. Once an egg was opened and the earth contents revealed, the skuas left the egg. There were no other predators that might have disturbed the eggs.

Experiment one was repeated twice. There were no significant differences between treatments (a) and (b) nor between treatments (c) and (d) (cf. Andersson and Wiklund, Anim. Behav. 26:1207–1212, 1978). Eggs in petrel nests (treatments [c] and [d]), however, were taken more rapidly than eggs placed on the ground (treatments [a] and [b]). After one hour, 6 of 20 eggs placed in nests had been taken compared with 3 of 20 eggs on the ground. After six hours, 17 of 20 eggs placed in nests had been taken compared with 7 of 20 eggs on the ground ($\chi^2 = 10.42$, df = 1, $P < 0.01$).

In Experiment two, 10 Southern Giant Petrel nests were removed from the petrel colony and placed as five pairs 50 m from the edge of the penguin colony. The two nests of a pair

were 2–3 m apart. One Macaroni Penguin egg was placed in each nest. Each pair of nests included one nest holding an empty egg with the hole visible and uppermost ("broken egg") and another nest containing an earth-filled egg with the hole invisible ("intact egg"). The eggs were checked 1, 2, and 6 h after placement. The experiment was repeated twice, at intervals of five and three days. On the nine occasions (out of 15 pairs of nests) that the first egg taken could be identified, the intact egg was always taken before the broken egg (Binomial test, $P = 0.002$), which was left alone. On three occasions both eggs were taken by the time of the same hourly check, but on the three occasions neither egg was taken after 6 h.

The two experiments demonstrate that skuas take eggs placed within nests more rapidly than eggs placed on the ground, and that intact eggs are taken more rapidly than broken eggs. The skuas' ability to use the cues of prey condition and location ensures that they usually concentrate their search on the most profitable eggs, namely those within the colony. But broken eggs also were occasionally taken. This may be the result of errors in recognition, or it may be an instance of the sampling behaviour that enables skuas to discover and then exploit new sources of food.

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Early autumn movements and prebasic molt of Swainson's Thrushes.—It is generally assumed that most north temperate migratory passerines, other than some flycatchers and swallows, molt in the vicinity of their breeding areas and then migrate (Dwight, Ann. New York Acad. Sci. 13:73–360, 1900; Payne, pp. 104–155 *in* Avian Biology, Vol. 2, D. S. Farner and J. R. King, eds., Academic Press, New York, New York, 1972). Here I present molt data for adult Swainson's Thrushes (*Catharus ustulatus*) that were captured during late July to mid-September at sites away from their breeding range.

Molt data for Swainson's Thrushes were collected from three banding stations: Berne, Albany County, New York; Long Point Bird Observatory (LPBO), Long Point, Ontario; and Prince Edward Point Bird Observatory (PEPT), Prince Edward Point, Ontario. At Berne I operated about 15 mist nets daily during late July through mid-September 1982, and from mid-August to early September 1983. Data were collected using a system similar to that of the British Trust for Ornithology (BTO) molt card (Snow, British Trust for Ornithology Field Guide No. 11, 1967) whereby the stage of molt of each flight feather is scored on a scale of 0–5 (see Cherry and Cannell, J. Field Ornithol., in press). My method differs from the BTO scores in that 1 = feather missing or in pin, and 2 = feather breaking out of pin to less than one-third grown. The BTO system was used at LPBO in 1977 and 1978, and at PEPT in 1979. Not all birds captured at LPBO and PEPT were examined for molt. I

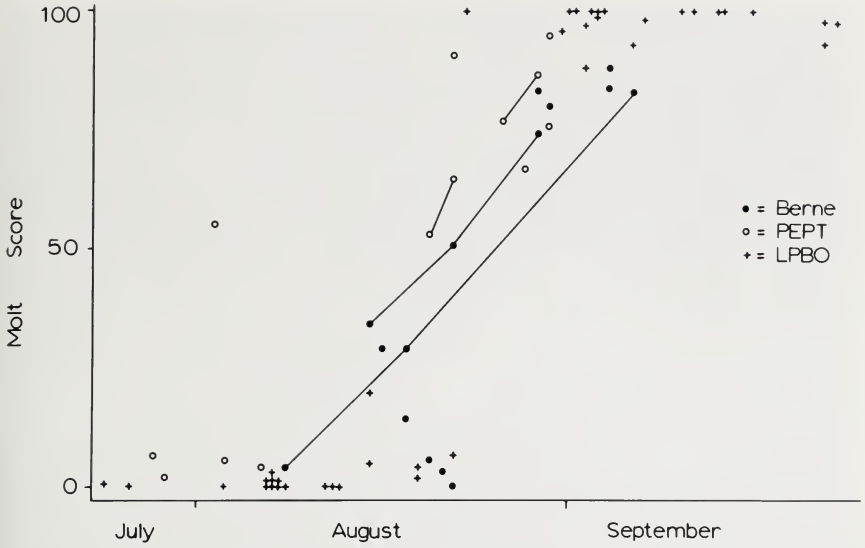

FIG. 1. Molt score (percent of flight-feather molt completed) plotted against date of capture for adult Swainson's Thrushes captured at three banding stations away from the breeding grounds. Solid lines connect recaptures of individual birds.

calculated molt scores for individual captures by summing the codes for all the flight feathers and then converting the sum to a percentage of 240 (240 is the maximum possible sum: the vestigial tenth primary was not included). Thus, the molt score is an estimate of the percent of flight-feather molt complete at that time.

Swainson's Thrushes do not breed at any of the banding locations. The portion of the breeding range nearest to LPBO is about 250 km N (Godfrey, Birds of Canada, Nat. Mus. of Canada Bull. No. 203, 1966). Although Godfrey (1966) shows that the breeding range includes the PEPT area, data from the Ontarior Breeding Bird Atlas Project show no breeding records in the counties of Prince Edward, Hastings, Lennox and Addington, Frontenac, and Leeds (R. Weir, pers. comm.). The nearest breeding area is probably 150 km N. In eastern New York, Swainson's Thrushes breed in the Adirondack and Catskill mountain regions (Bull, Birds of New York State, Doubleday, New York, New York, 1974). Berne is near the northern Catskills, and Bull (1974) shows that the breeding range extends very close to Berne. K. P. Able and I have worked extensively in southwestern Albany County and have never encountered Swainson's Thrushes between the first week of June and the end of July.

There were 15 captures of 10 individual Swainson's Thrushes for which molt data were taken at Berne in 1982 and 1983; 13 captures of 11 individuals at PEPT in 1979; and 39 captures of 39 individuals at LPBO in 1977 and 1978. Fig. 1 shows the molt scores of these birds plotted by date of capture. Four birds were recaptured within a month of their first capture, and from these I calculated a mean molt rate of 3.1% per day following the methods of Cherry and Cannell (in press). At this rate it would take 32 days to complete flight-feather molt. The bird that stayed at Berne from 8 August to 6 September 1982 was encountered again at Berne on 16 August 1983 with a molt score of 24, two days ahead of its molt schedule of 1982.

These data show that some Swainson's Thrushes leave their breeding areas before starting to molt, or when they are still in the early stages of molt. The proportion of the population that does this is unknown. In some cases the birds I examined must have moved at least 250 km from their breeding sites, although birds captured at Berne may have moved only 30 km. The pattern of captures suggests that Swainson's Thrushes are less likely to move during the middle of molt.

I thank LPBO and PEPT for providing unpublished banding data. R. Smith and H. Quilliam helped me extract the data, and R. Weir provided information on the breeding status of Swainson's Thrush in the PEPT area.—Jeffrey D. Cherry, *Dept. Biol. Sci., State Univ. New York, Albany, New York 12222.* *Accepted 10 Mar. 1985.*

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Nest-defense of the Florida Scrub Jay and the problem of "incubation" by male passerines.—Wyckoff (Wilson Bull. 95:472, 1983) reported "the first record of incubation behavior by a male" Chestnut-collared Longspur (*Calcarius ornatus*). She may have observed nest-defense behavior instead.

Grimes (quoted by Sprunt *in* Bent, U.S. Natl. Mus. Bull. 191:77–88, 1946) believed erroneously that the male Florida Scrub Jay (*Aphelocoma c. coerulescens*) performed incubation, although Amadon (Am. Mus. Novitates 1252:1–22, 1944) had correctly reported that only females incubate. Only the female of this species develops an incubation patch. As noted by Woolfenden (Living Bird 12:25–49, 1974), Sprunt probably wrote his contribution before Amadon's paper appeared, and Grimes' mistake "most likely originates from observing nest-defense behavior by the male."

Nest-defense by the Florida Scrub Jay is similar in the sexes and may be described as follows, based on our separate and joint observations over many breeding seasons at Archbold Biological Station, Lake Placid, Highlands Co., Florida. The most commonly observed occurrence is upon an observer's approach to a nest in which the female is incubating or brooding. Whether the breeding female or male defends is a matter of individual variation, probably depending in part on how bold the birds are with respect to human intruders; we frame our description in terms of the male. The defending male flies to the vicinity of the nest whether or not the female flushes, and either before or after she departs if she does flush. If she departs and he lands adjacent to or on the nest, he often looks down into it as if to inspect its contents. Sometimes he stands on a branch adjacent to and usually a little higher than the top of the nest, often a little forward of the nest in the direction of approach by the observer. He may also stand on the nest-rim itself or upon the female if she remains. Most often on close approach by an observer to a nest from which the female has fled, the male jay straddles the nest contents, placing his feet on the inside of the nest-rim, and drops his body low over the eggs or nestlings.

Whatever his position relative to the nest, the defending male adopts a characteristic posture. His gray crown feathers are depressed strongly as the bird faces the intruder, and his "eyebrow" feathers protrude laterally, forming a ridge over the eye that gives the bird a "scowling" appearance. His body feathers are erected somewhat, especially on the flanks, making the male seem larger than usual, and his folded wings are held out at the carpal joints (Figs. 1, 2). Sometimes his tail is spread and sometimes it is not. The male is silent while in this posture, and he may remain over the nest for as long as observers are nearby,

FIG. 1. Male Florida Scrub Jay in nest-defense posture on nest. Note depression of crown feathers, erection of body feathers, and holding of wings out at the carpal joints. (Photo by JPH of breeding male SRW- on 21 April 1981.)

and for some minutes after they leave the immediate area and watch from afar with binoculars. During such lengthy periods of defensive behavior, the male may give the appearance of incubating or brooding, but he does not settle far enough down upon the nest contents to be pressing against eggs or young. By contrast, an incubating female that is not defending settles farther down on the nest, does not have crown feathers sleeked, and does not hold her wings out at the carpal joints (except in response to hot conditions).

Wyckoff's (1983) male longspur may have been defending the nest on the four occasions of reputed incubation she reported. On the first (3 June), the male circled and vocalized upon approach of the observer, and settled on the nest when the female flushed; the observer watched from 3.6 m away. The maximum time the male could have been on the nest was the 14 min from 11:09 through 11:22. On 4 June the male was flushed from the nest, to which he may have gone upon approach of the observer. On 5 June the male was on the nest for 5 min, and on 6 June was seen on the nest. No details are provided that would confirm actual incubating behavior by the male, and the circumstances of the observations (approach of the observer, retreat of the female, circling by the male, vocalizing by the male, short stays on the nest) all suggest that the male may have been defending rather than incubating.

Many families of passerine birds include species in which the male is reported to incubate. No doubt many of these reports are accurate, but it seems likely that others could have resulted from observers mistaking defensive behavior for incubation. When there is no evidence concerning incubation patches in the sexes, behavioral observations are useful data. However, reputed male incubating behavior by any sexually dichromatic species such

FIG. 2. The same male as in Fig. 1, lowered in the nest-cup in a position that could be mistaken for incubating or brooding behavior. Note that the body is not sufficiently lowered to be pressing against eggs or nestlings.

as the Chestnut-collared Longspur should be immediately suspect if the male wears brightly colored, display plumage and the female is concealingly colored. As the case of the Florida Scrub Jay shows, even sexually monomorphic birds may have division of labor in incubation. Therefore, we recommend that all reports of suspected male incubation in passerine birds be accompanied by sufficient observational details to rule out nest-defense as a possibility.—JACK P. HAILMAN, *Dept. Zoology, Univ. Wisconsin, Madison, Wisconsin 53706;* AND GLEN E. WOOLFENDEN, *Dept. Biology, Univ. South Florida, Tampa, Florida 33620.* *Accepted 25 Mar. 1985.*

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Nestling feeding schedules of Turquoise-browed Motmots in Yucatán, Mexico.—Skutch (Auk 62:489–517, 1945; Auk 64:201–217, 1947; Ibis 106:321–332, 1964; Wilson Bull. 83: 74–94, 1971) and Orejuela (Living Bird 16:193–208, 1977) have provided data on schedules maintained by adult members of the family Momotidae during provisioning of their young. For the Turquoise-browed Motmot (*Eumomota superciliosa*), one of the two most common members of this family, Skutch's (1947) data do not include nestling weights, and both he (1947) and Orejuela (1977) only provide data for portions of the first posthatching week. Here, we augment those data and supplement information provided by Scott and Martin (Biotropica 15:8–14, 1983) on other aspects of reproduction of this species in central Yucatán

TABLE 1

NESTLING FEEDING SCHEDULES OF TURQUOISE-BROWED MOTMOTS DURING SECOND WEEK POSTHATCH, JUNE 1984, AT UXMAL, YUCATÁN

Nestling age (days)[a]	Date	Time (h)	Disturbance[b]	Number of visits			Visits per hour		
				#1[c]	#2	Total	#1	#2	Total
7–8	20	07:38–10:42	–	10	11	21	3.2	3.5	6.7
		15:06–17:18	–	2	13	15	0.9	5.9	6.8
8–9	21	08:23–10:39	0	11	8	19	4.8	3.5	8.3
		10:43–11:59	+	4	3	7	3.1	2.3	5.4
		08:23–11:59	<+	15	11	26	4.2	3.1	7.2
		16:58–18:47	0	5	9	14	2.8	5.0	7.8
9–10	22	07:41–08:37	0	3	8	11	3.3	8.9	12.2
		08:37–08:59	+	2	1	3	5.4	2.7	8.1
		07:41–08:59	<+	5	9	14	3.8	6.9	10.8
10–11	23	05:48–07:31	0	6	14	20	3.5	8.2	11.8
		17:03–18:03	0	3	13	16	3.0	13.0	16.0
11–12	24	17:14–18:36	0	2	13	15	1.4	9.3	10.7

[a] For 2 oldest young. (Hatching is asynchronous in this species.) Estimates were based on nestling morphology and weights recorded on 21 June and on comparisons with similar data taken in Yucatán (Scott, unpubl. M.A. thesis, Univ. Texas, Austin, Texas, 1984) and Campeche (Orejuela 1977).

[b] Disturbance: 0 = no human disturbance observed; – = few humans present, separate data not recorded; + = presence of humans seemed to delay flights from reconnaissance perch; <+ = presence of humans sometimes delayed flights from reconnaissance perch.

[c] Parents were unsexed but color marked.

by providing weight-related feeding rates and associated information for midportions of the nestling period.

On 20 June 1984, we began observations of an unsexed color-marked pair of Turquoise-browed Motmots attending four nestlings at Uxmal, Yucatán (20°20′N, 89°46′W). Scott and Martin (1983; Biotropica 16:319–323, 1984) have provided detailed climatological, physiographic, and ecological descriptions of this site and the surrounding area. The forest and clearings were "green" during our study; and insects, the primary food of nestling motmots here, appeared abundant. The nestlings occupied a hole (vacant cross-beam socket), 2.33 m above floor level, in the wall of an elevated room off the east façade of an archaeological structure. The hole was located approximately 15 m distant from the outer entry to the room; timing of parental visits began and terminated when adults flew through this entry. The adults reconnoitered the site from perches at or near the forest edge before flying to the archaeological structure. Although visitation by custodians and tourists was infrequent during our observations, and the motmots here were habituated to man, we kept separate records for periods during which provisioning flights appeared to be delayed by the presence of humans. Observations were made through 8× binoculars; weights of nestlings were taken to the nearest g with a 100-g Pesola spring balance.

The earliest (with regard to nestling age) feeding rates we recorded, those for 7–8-day-old young (6.7, 6.8 visits/h, Table 1), exceeded that observed by Orejuela in 1977 (5.3 visits/h) for 6-day-old Campeche nestlings of this species, and that recorded by Skutch (1947) for 7-day-old young in Honduras. On 21 June, at 08:00, the Uxmal nestlings weighed 40, 36, 33, and 29 g. Feeding rates generally increased with age of young (Table 1), and when the nestlings were only 10–11 days old, feeding rates exceeded that reported by Skutch (1964)

for 19-day-old *Momotus momota* (11/h). One parent (#2) visited with signficantly greater frequency than the other ($\chi^2 = 16.86$; df = 1, $P < 0.005$; excluding visits affected by human disturbance), but this division of effort may not be representative of that over an entire day. Mean time spent per visit (room entry to exit) was 79.5 sec (N = 123; SE = ±4.7 sec). Few food items carried could be identified, but adult lepidopterans (≥3 species) represented at least 13% of provisions. At 17:30, 24 June, the (unmarked) nestlings appeared healthy and weighed 45, 43, 41, and 33 g; they had collectively gained 24 g during the preceding 3 days. Observations of this brood were terminated well before its projected potential fledging date.

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Arrival and departure patterns of Great Blue Herons at a South Dakota colony.—Two of the potential benefits of colonial nesting or roosting are predator protection (Lack, Ecological Adaptations for Breeding in Birds, Methuen and Co., London, England, 1968) and the use of the colony or roost as an "information centre" (Ward and Zahavi, Ibis 115:517–534, 1973). Weatherhead (Am. Nat. 121:237–243, 1983) recently suggested that the principal advantages of communal roosting may differ among birds in the same roost. Central roosters may benefit more from predator protection provided by roosting, rather than from information exchange, whereas less-dominant birds roosting on the edge may derive the most benefit from information exchange on favorable feeding sites. Evans (Auk 99:24–30, 1982) hypothesized that colonies in group-foraging birds may play an important role in preventing dispersal of foraging individuals by serving as central assembly points.

The Great Blue Heron (*Ardea herodias*) has been discussed as a colonial nester that may use the colony as a source of information on feeding areas (for differing opinions see Krebs, Behaviour 51:99–134, 1974; Pratt, Wilson Bull. 92:489–496, 1980; Bayer, Auk 98:589–595, 1981). Weatherhead's (1983) "two-principle strategies" hypothesis may provide an explanation for these differences.

Here, we report on departure directions, arrival and departure frequencies, the degree of colony synchrony, and the extent of clumping at arrival and departure from a colony of Great Blue Herons.

Study area and methods.—We observed arrivals and departures of Great Blue Herons at the Glendale heronry on the James River in Spink County, South Dakota. The heronry consisted of 66 active nests, all of which were visible from a blind constructed in a tree 50 m across the river from the heronry. A large opening allowed a view of the heronry, and smaller openings permitted the viewing of all birds approaching or departing from the colony. Observations were made from the blind from sunrise to sunset once each week from May through August 1980 for 156 h; the number of active nests did not change substantially

during this time. Time and flight direction (N, NE, E, SE, S, SW, W, NW) were recorded for all nest departures and arrivals.

To determine the extent of clumping during arrivals and departures, each arrival or departure was placed in one of four categories: (1) an arrival from the same direction as the most recent arrival; (2) an arrival from a different direction than the previous arrival; (3) a departure in the same direction as the previous departure; or (4) a departure in a different direction than the most recent departure. Times between successive arrivals or departures were measured in 1-min intervals. The arrival and departure patterns within the four categories were tested statistically using a Chi-square analysis described by O'Malley and Evans (Can. J. Zool. 60:1024–1031, 1982) in work on White Pelicans (*Pelecanus erythrorhynchos*) in Manitoba. This method tests for clumping by testing arrival and departure distributions for randomness and is applicable to our study because, as in their study, our data were derived from observations of an inland colony, not influenced by tides.

In an effort to determine more precise departure directions, observations were also made from a hill located approximately 110 m northwest of the heronry. All departures except those due east and due south were observable from this vantage point. Another observer was stationed so that he or she could see herons departing east and south. Information recorded at these sites included the time of departure and a compass reading of the point at which a bird disappeared. These data were collected once each week from sunrise until 2 h after sunrise for 2 consecutive breeding seasons in 1980 and 1981 and were used only in calculation of predominant flight lines.

The relationship between arrivals/h and hour of the day was analyzed by analysis of variance. Potential relationships between arrivals/h and hour of the day were analyzed using regression analyses testing the linear, quadratic, cubic, and quartic models. Analyses of arrivals and departures were divided into early (15 May–12 June) and late (20 June–29 July) portions of the 1980 breeding season.

Arrival and departure rates, synchrony, and direction.—Herons arrived at the colony at an average rate of 12.4 herons/h. The average departure rate was 10.1 birds/h. Maximum hourly arrival and departure rates were 51 herons/h and 45 herons/h, respectively. Theoretically, arrival and departure rates should be similar, as each arrival will presumably be followed by a departure and vice versa. The difference in the arrival and departure rates can be partially explained by human sampling error. An arriving bird emits a "landing call" when returning to the nest to alert its mate (Mock, Wilson Bull. 88:185–230, 1976), making arrivals easy to detect. On the other hand, birds depart quietly and occasionally may have been missed by observers during periods of great activity in the heronry.

Colony synchrony can be measured by dividing hourly arrival or departure rates by the total number of breeding herons (Bayer 1981). The average degree of colony synchrony for arrivals was 9.4% of breeding birds/h and 7.6% for departures. The maximum arrival and departure synchrony rates were 38.6% and 34.1% of breeding birds/h, respectively.

Bayer (1981) defined the average time between an individual bird's arrival or departure as the inverse of the mean of the average hourly arrival and departure rates. The mean of the average hourly arrival rate was 0.09 arrivals/heron/h of observation. The corresponding departure rate was 0.08 departures/heron/h of observation. An average of 11.1 h elapsed between an individual's arrivals and 12.5 h between an individual's departures.

Relationships between arrival and departure and time of day.—The relationship (ANOVA) between total arrivals/h and the different hours of the day (06:00–21:00) did not differ significantly in either the early or late portions of the breeding season. Departures for the early period were significantly related to hour of the day (ANOVA; $F = 1.97$, $P = 0.04$) but departures for the late period were not significantly related to time of day. When departures/h for the early period were regressed against hour of the day, the quadratic model, which

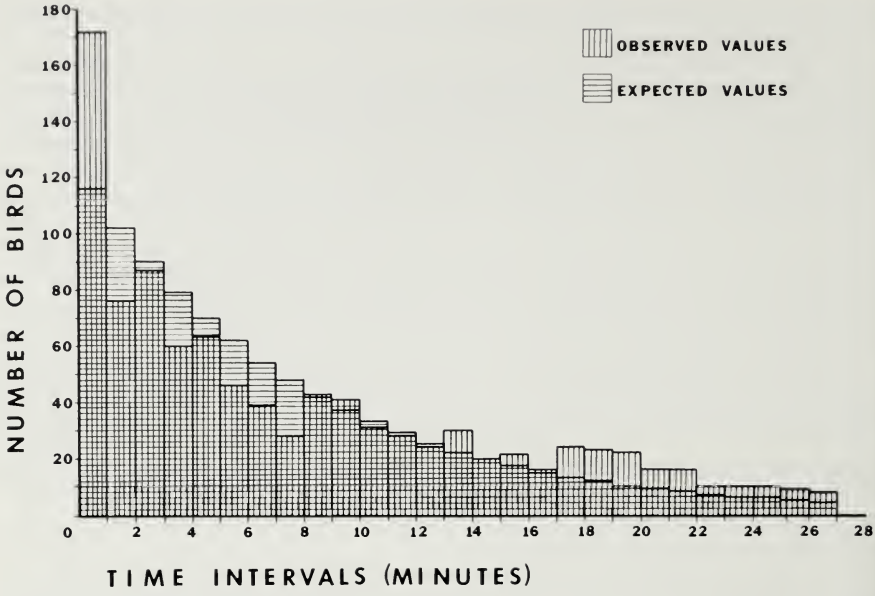

FIG. 1. Observed and expected (based on O'Malley and Evans, Can. J. Zool. 60:1024–1031, 1982) departure frequencies of Great Blue Herons flying in the same directions from the Glendale heronry in 1980.

explained 24.9% (N = 62) of the variance, was significantly better than the linear model; the cubic and quartic models provided no significant improvement over the quadratic model.

Arrival and departure clumping.—Departures in the same directions were nonrandomly distributed in time ($\chi^2 = 112.62$, df = 25, $P < 0.005$) (Fig. 1); however, departures in different directions also exhibited a clumped distribution ($\chi^2 = 201.29$, df = 25, $P < 0.005$). A similar clumped pattern resulted from the analysis of arrivals from the same directions ($\chi^2 = 200.97$, df = 25, $P < 0.005$) and arrivals from different directions ($\chi^2 = 201.29$, df = 25, $P < 0.005$). Using Bayer's (1981) definition of a flock as a group of birds departing one min or less apart, roughly one-third of Glendale colony herons arrived and departed in flocks. Thirty-five percent of arrivals and 28% of departures occurred in flocks.

Discussion.—Data presented here on colony synchrony and average times between an individual bird's arrivals or departures suggest that Glendale colony herons arrived and departed infrequently and solitarily. This conclusion is misleading, however, as these figures represent averages. The fact that arrivals and departures were clumped in both the same and different directions indicates that a significant number of birds tended to arrive and depart in flocks but did not necessarily follow each other to and from feeding areas. Although some researchers have discussed relationships between Great Blue Herons' departures and time of day (Brandman, Ph.D. diss., Univ. California, Los Angeles, California, 1976; Warren, M.S. thesis, Univ. Idaho, Moscow, Idaho, 1979), our analysis indicated that arrivals or departures could not be predicted well on the basis of time of day.

Herons demonstrating clumping during departures from heronries with a few predominant flight lines will likely show significant departure clumping in the same direction. The Glendale

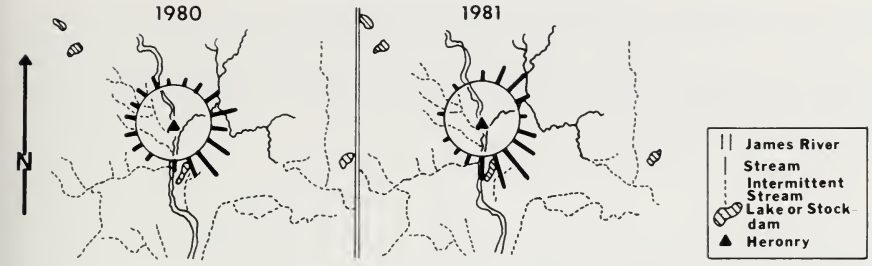

FIG. 2. Relative distribution of departure directions to nearest 20° interval based on points of disappearance of herons from the Glendale heronry in 1980 and 1981.

colony had from 6–8 predominant flight lines and numerous lesser routes (Fig. 2). Part of the directional clumping of arrivals and departures in our study may have been related to use of these dominant flight lines. One possible explanation of the significant arrival and departure clumping by Glendale colony herons may be provided by findings (Pratt 1980) based on observations of a California heronry. Pratt (1980) reported that the timing of nest departures was dependent on the times at which nest relief occurred. Assuming that herons spend a similar amount of time in the process of nest relief and that they tend to arrive in flocks, birds would also tend to depart in flocks.

Krebs (1974) reported that herons leaving a colony in British Columbia tended to depart in groups and shift from one area to another in unison. DesGranges (Proc. Colonial Waterbird Group 2:192–201, 1978) found that successive departures from a Quebec colony were usually in the same direction, leading him to conclude that the birds were using the colony as an information source on local feeding conditions. Bayer (1981) and Pratt (1980) found that herons in their respective studies did not follow each other to feeding areas.

Although some herons in the Glendale colony may have been following others to foraging sites, clumping of departures in the same and different directions indicates that other factors are involved. Clumped arrivals from the same and different directions cause similar interpretation difficulties. We suggest that the information hypothesis provides at best a partial explanation for arrival clumping in the Glendale colony.

Weatherhead's (1983) "two-principle strategies" hypothesis would explain directional departure clumping in some, perhaps subordinate, birds, while not suggesting that all birds follow others for foraging reasons. We feel the departure and arrival patterns in the Glendale colony may indeed reflect social relationships and may differ considerably among individual herons. Some clumping of arrivals and departures in the same direction could be explained by the predominance of several flight paths over others (Bayer, Auk 99:31–40, 1982). Because of the lack of group foraging in Glendale colony herons, we did not feel Evans' (1982) hypothesis was applicable. We suggest that much clumping of departures or arrivals may occur simply through social facilitation of "flight-primed" birds that take flight after observing other colony or feeding area departures (Bayer 1982); this could explain the clumping observed in both arrivals and departures. As suggested by Bayer (1982), flights involving information exchange are socially facilitated, but all socially facilitated flights need not involve information exchange.

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proved for publication by the Director, Agricultural Experiment Station, South Dakota State University, as Journal Series No. 1940.—Eileen M. Dowd, *Missouri Dept. Conservation, 1110 College Avenue, Columbia, Missouri 65201,* and Lester D. Flake, *Dept. Wildlife and Fisheries Sciences, P.O. Box 2206, South Dakota State Univ., Brookings, South Dakota 57007.* *Accepted 21 Jan. 1985.*

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Notes on the relationships of island area and distance from mainland to the presence of Herring Gull colonies in Lake Nipigon, Ontario.—Breeding colonies of most gulls and terns are more common on islands than on mainland (Bent, U.S. Natl. Mus. Bull. 113, 1921; Tinbergen, The Herring Gull's World, Basic Books, New York, New York, 1961). This observation is most often explained in terms of avoidance of predation (Strong, Auk 31: 22–49, 178–200, 1914; Burger and Lesser, Ibis 120:433–449, 1978). Avoidance of predation by birds (e.g., American Crows, *Corvus brachyrhynchos*; Common Ravens, *Corvus corax*; Great Blue Herons, *Ardea herodias*) and by mammals (e.g., humans; dogs, *Canis familiaris*; red fox, *Vulpes vulpes*; mink, *Mustela vison*; otter, *Lutra canadensis*) may be important in explaining the island preference of Herring Gulls (*Larus argentatus*) (cf. Harris, Ibis 106: 432–456).

Other factors are involved in colony selection by gulls and terns, such as proximity to feeding areas, vegetation type and plant density (Burger and Lesser, 1978), height above water level (McNicholl, Auk 92:98–104, 1975; Southern, Auk 94:469–478, 1977), exposure to open water (Burger and Lesser, 1978), and suitability of nesting substrates (Ludwig, Auk 91:575–594, 1974).

The reconnaissance nature of this study precludes discussion of the relative influences upon colony selection of factors other than island area and distance from mainland. This paper reports on the relationships of island area and distance from mainland to the presence of Herring Gull breeding colonies in Lake Nipigon, Ontario.

Methods.—Research was conducted along with a study of the island biogeography of seed plants in Lake Nipigon. The area is described by Timoney (Can. Field-Nat. 97:16–25, 1983).

From mid-June to mid-August 1979, the presence or absence of Herring Gull breeding colonies was noted for 48 islands. A colony or pair was recorded present if at least one nest with incubated eggs or young was observed. If no nests, or only abandoned nests were observed, no colony was recorded. Island areas were determined by planimeter from Canada NTS maps (scale = 1:50,000). Distance from mainland was measured as the shortest distance between an island's shore and the mainland shore.

Results.—Islands ranged in size from <0.1 ha to 19.4 ha and in distance from mainland from 50 m to 10.5 km. Distance from mainland and island area were not correlated significantly ($r = 0.22$, $0.2 > P > 0.1$). No mainland colonies were found.

Island area bore no linear correlation with presence–absence of Herring Gull colonies (Kendall's Tau, two-tailed P, Mann-Whitney U-test: $\rho = 0.05$, $P = 0.76$). The six smallest islands (all <0.1 ha) also were the lowest and flattest and were subject to inundation. None of these low-lying islands supported a Herring Gull colony. Timoney observed waves or spray saturating four of these islands. The meager heights above water and the near barrenness of the other two small islands (with only mosses and *Potentilla norvegica* in rock cracks, and saxicolous lichens) suggest that they too were inundated regularly.

Even with these six smallest islands omitted, area (ranging from 0.1 to 19.4 ha) was still not correlated significantly with Herring Gull colonies ($\rho = -0.19$, $P = 0.32$).

The rank correlation statistics tested for a linear relationship between colony presence and area; but, as Burger and Lesser (1978) have shown for Common Terns (*Sterna hirundo*), islands intermediate in size may be preferred. Harris and Matteson (Univ. Wisconsin Sea Grant Technical Report No. 227, 1975) found the densest Herring Gull colonies in Lake Superior on islands intermediate in size. The two densest colonies found on Lake Nipigon were on intermediate-sized islands (0.4, 1.1 ha).

The data suggest that islands between 0.1 and 6.0 ha may be more favorable nesting sites than islands <0.1 or >6.0 ha (Kruskal-Wallis test, $\chi^2 = 6.9$, df = 2, $0.05 > P > 0.03$). No breeding colonies were observed on the six islands <0.1 ha, while 17 of the 35 islands between 0.1 and 6.0 ha supported Herring Gulls. Of the seven islands >6.0 ha, one supported Herring Gulls. Conclusions based on these results should be considered tentative as non-significant results ($P > 0.10$) were obtained when tests were run on data split into various objective size classes.

Herring Gulls on Lake Nipigon seem to nest on islands intermediate in size. Small islands are subject to inundation and colonies on large islands may be more susceptible to predation.

The occurrence of Herring Gull breeding colonies was correlated positively with distance from mainland ($\rho = 0.47$, $P = 0.0032$). All 12 sample islands within 1.1 km of the mainland lacked colonies, and all four islands beyond 6.5 km supported colonies. Islands supporting Herring Gull colonies were located significantly farther from the mainland than islands lacking colonies (Kruskal-Wallis test, $\chi^2 = 8.6$, df = 1, $P < 0.005$). The average distance from mainland of the 18 islands supporting Herring Gull colonies was 4.0 km (SD = 2.8), and that for the 30 islands lacking colonies was 1.9 km (SD = 1.8).

Acknowledgments.—We thank R. Kowal for his enthusiasm and his modification of Kendall's Tau to accommodate ties in the ranks. R. Kowal, R. Howe, and anonymous reviewers provided helpful criticism of the manuscript.—Kevin Timoney, Jim Rogers, and Anne Robinson, *Dept. Botany, Univ. Alberta, Edmonton, Alberta T6G 2E9, Canada.* *Accepted 13 Feb. 1985.*

Wilson Bull., 97(3), 1985, pp. 379–381

Interactions between House Sparrows and Common Ground-Doves on Walker's Cay, Bahamas.—Between 14 and 16 March 1984, we observed at least eight male and seven female House Sparrows (*Passer domesticus*) around the hotel on Walker's Cay (27°17′N, 78°25′W) at the north end of the Bahama Islands. Previous records of House Sparrows from the Bahamas have included an unsuccessful introduction at Nassau on New Providence in the 1870s (Brudenell-Bruce, The Birds of the Bahamas, Taplinger Publ. Co., New York, New York, 1975) and scattered records of individuals on New Providence and Grand Bahama (Brudenell-Bruce, 1975, American Ornithologists' Union, Check-list of North American birds, 6th ed., Allen Press, Lawrence, Kansas, 1983). Recent records are believed by Brudenell-Bruce to be of birds that had "stowed away" on boats from Florida. Emlen (Ornithol. Monogr. 24, 1977:128) lists House Sparrows as "common . . . permanent residents in urban Freeport and around hotels," although none was seen on his transect routes on Grand Bahama. Emlen (1977:9) also recorded the species on other north, south, and east

Bahama islands, but provides no details. Buden (Ph.D. diss., Louisiana State Univ., Baton Rouge, Louisiana, 1979) did not record House Sparrows from the southern Bahamas.

We were unable to learn either the origin of the birds or the length of time that the House Sparrows have been present, but from their numbers we assume they had nested successfully on Walker's Cay. There are regularly scheduled airline flights from Ft. Lauderdale, Florida, and the island is a frequent stopover for large sport-fishing and cargo boats from Florida, any of which could bring birds from the mainland. The birds might also have arrived on inter-island ferries from Grand Bahama or other populations. Finally, Broun (Auk 89:187–189, 1972) presents evidence of migratory movements of House Sparrows, and an alternative hypothesis is that the population on Walker's Cay resulted from natural dispersal of birds that might have accompanied migrant species from the mainland. Woolfenden and Robertson (Florida Field Nat. 3:23–24, 1975) summarize evidence to suggest that such was the case for a breeding population established briefly on the Dry Tortugas.

On 16 March, at 14:00, we observed a male House Sparrow carrying a piece of dried grass to a 40-cm-high × 25-cm-wide mass of dried grasses. The nest was ca 9 m up in a 10-m strangler fig (*Ficus* sp.). Subsequently two males simultaneously brought grasses to the same structure—one to an entrance near the top and another to an entrance on the underside. The males often perched near these entrances and within 25 cm of one another without interacting.

At 14:15 we noticed a Common Ground-Dove (*Columbina passerina*) nest on a horizontal limb 5 m up in the same tree and about 8 m from the sparrow nest. The female dove was on the nest, and the male had just flown from the ground with a piece of dried grass. As the male dove arrived at the nest, one of the male House Sparrows flew from its nest and landed 10 cm from the dove nest. It seized the end of the dove's piece of grass in its beak, whereupon the dove relinquished it, and the sparrow flew to the upper part of the sparrow nest and added it to the structure. The dove then flew to the ground for another piece of grass and flew back to its nest. The male House Sparrow flew to within a meter of the dove nest, but the dove had already given the grass to its mate on the nest, and she was incorporating the grass into the nest. The sparrow remained close and, in the next 6 min, the dove made 7 more trips with grass and was met twice more by the male House Sparrow who took the grass and added it to the upper part of the duplex sparrow nest. At no time did either dove resist the robbery.

After the loss of the third piece of grass, the doves left together and flew to the ground 50 m away. They did not return to the nest site during the next hour, although they did return to the nest tree to copulate on a branch 5 m from their nest and 5 m below the sparrow nest.

At 14:45 both male House Sparrows were away from the nest tree when a female House Sparrow flew to the lower part of the sparrow nest and removed two pieces of grass, dropping them to the ground. She then flew to the dove nest and began pulling grasses from it, also dropping them to the ground. A male House Sparrow then flew to a branch ca 1 m above the dove nest where it began calling and preening. The female sparrow also began preening, stopping every 3–4 min to pull a piece of grass from the dove nest and drop it. Within 30 min the dove nest was completely dismantled. At 15:30 both sparrows left the tree, and our observations were terminated.

Our observations are of significance not only because of the novelty of House Sparrows in the Bahamas and of their stealing nest material from the Common Ground-Doves, but also because of the "duplex" tree nest, and the lack of response from the doves. Summers-Smith (The House Sparrow, Collins, London, England, 1963:53) notes that tree nests are used when other sites are not available and reports up to 17 nests in a single tree (p. 55). He adds, however, that tree nests are "usually well separated" (plate 12) and that House

Sparrow males, while not maintaining large territories, do defend their nests vigorously against other male House Sparrows (p. 57). At no time was any sign of aggression shown by the male House Sparrows at this duplex nest.

Brudenell-Bruce (1975:67) noted that Common Ground-Doves in the Bahamas were very aggressive and belligerent toward other species, a trait that certainly was not manifested in this instance.

Concern has frequently been expressed for the potential negative impact of introduced House Sparrows on native cavity-nesting birds (e.g., Jackson and Tate, Wilson Bull. 86: 435–449, 1974). Our observations suggest that under some conditions they also may have a negative impact on noncavity-nesting species. This might be particularly true on an island such as Walker's Cay (total area ca 40 ha) where populations of all species are very small.

The paucity of information concerning the distribution and status of this species in the Bahamas is disconcerting. Available information suggests that the species has either been overlooked or is rapidly expanding its range. In view of the House Sparrow's impact in other parts of the world and its importance as a subject of evolutionary studies (e.g., Johnston and Selander, Am. Nat. 107:373–390), we feel that the status of Bahamian populations is worthy of further study.—Jerome A. Jackson and Bette J. Schardien Jackson, *Dept. Biological Sciences, Mississippi State Univ., Mississippi State, Mississippi 39762.* *Accepted 19 Jan. 1985.*

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Commentary and observations on the alleged transportation of eggs and young by caprimulgids.—Austin and Singer (Birds of the World, Hamlyn, London, England, 1961) state that "Nightjars are among the few birds that will move their eggs or young when disturbed or alarmed by the threat of discovery. This has been questioned ever since Audubon described a Chuck-will's-widow moving its eggs in its capacious mouth a century ago. But the phenomenon has been observed in this species often enough since to validate it."

Commentary.—Statements such as the one above persist in the ornithological literature despite the fact that there is no satisfactory evidence that anyone since Audubon (Ornithological Biography, I, Edinburgh, Scotland, 1831) has seen a Chuck-will's-widow (*Caprimulgus carolinensis*), or any other nightjar for that matter, carrying an egg in its mouth. Several ornithologists have deliberately tried to induce Chuck-will's-widows to perform this feat by handling the eggs and provoking the birds, yet none has succeeded (Ganier, Wilson Bull. 76:19–27, 1964). After a critical reading of Audubon's biographies, Ganier (1964) concluded ". . . it is my belief that Audubon had no such personal experience on which to base this story. It does not fit in with my own long experience with these birds, nor have I been able to find in the literature any ornithologist since Audubon's time who claims to have witnessed such an episode."

Extensive studies of Common Nighthawks (*Chordeiles minor*) by Weller (Auk 75:48–59, 1958), of Pauraques (*Nyctidromus albicollis*) by Skutch (Parent Birds and Their Young, Univ. Texas Press, Austin, Texas, 1976) and of Whip-poor-wills (*Caprimulgus vociferus*) by Raynor (Bird-Banding 12:98–104, 1941) also failed to produce evidence for oral egg-carrying in these species.

In Africa, the Mozambique Nightjar (*C. fossii*) is credited with transporting an entire clutch in its bill (Mackworth-Praed and Grant, Birds of Eastern and North Eastern Africa, Longmans, London, England, 1952). I have been unable to trace the authority for this

statement; Armstrong (Bird Display and Behaviour, Dover Publications, New York, New York, 1965) cites Jackson (The Birds of Kenya Colony and the Uganda Protectorate, Gurney and Jackson, London, England, 1938), but I could find no mention of it in Jackson under any of the species discussed. In over 20 years of studying the nightjars of southern Africa, I have found no evidence of any nightjar carrying any eggs in its mouth. The "capacious mouth" of a nightjar could certainly accommodate an egg, perhaps even two, just as it could probably accommodate the teat of a goat, but there appears to be no more evidence of it being an egg-carrier than there is of it being a goatsucker.

Caprimulgid eggs are sometimes moved short distances by wind (Parks, Bird-Banding 18: 170, 1947), flood (Morgan, Aust. Bird Watcher 1:117–118, 1960), or the normal movements of the incubating bird (Woods, Condor 26:1–6, 1924), the cumulative effect of the latter occasionally resulting in moves of several meters from the original nest site (Gross, pp. 206–234 *in* Bent, U.S. Natl. Mus. Bull. 176, 1940). This could be mistaken for deliberate translocation. When the eggs disappear it is sometimes assumed that the birds have moved them to a new site (Cameron, Auk 24:289–406, 1907; Merrill, U.S. Natl. Mus. Proc. 1:118–173, 1878), especially when another clutch is found in the vicinity (Warren, Report on the Birds of Pennsylvania, Meyers, Harrisburg, Pennsylvania, 1890; Ferguson, Wilson Bull. 79: 452–453, 1967). It would be more reasonable to assume that the first clutch was taken by a predator and that the second clutch was a replacement clutch or belonged to a different bird. Some apparent movements or disappearances of eggs or young are due to observer error in recalling the exact position of the nest. These difficulties can be overcome by marking the eggs and birds and by accurately locating the nest position in relation to fixed reference points (see below).

Nightjars in flight have been seen carrying eggs beneath the body, apparently held between the legs or in the claws (Rysgaard, Auk 61:138, 1944; Kilham, Wilson Bull. 69:113, 1957; pers. obs.). It is clear from the detailed accounts of these incidents that all are the result of accidental transportation.

Field observations.—I studied the breeding biology of the Fierynecked Nightjar (*C. pectoralis*) and some related species on Ranelia Farm (19°22′S, 32°37′E, 885 m above sea level) near Mutare, Zimbabwe, from 1972 to 1975 in partial fulfillment of the requirements for a Master's degree (Jackson, M.S. thesis, Univ. Natal, Pietermaritzburg, South Africa, 1983). One of the study objectives was to obtain positive data on the transportation of eggs or young.

Study area and methods.—My study area of 100 ha consisted of miombo woodland (mainly *Brachystegia* and *Julbernardia* spp.) on gently sloping sandveld, broken by outcropping sheets and domes of granite. I established a network of fixed, numbered concrete beacons to serve as reference points for my field work. A closed traverse of the beacons was carried out by theodolite to provide the survey data for mapping the network. The exact location of every nightjar nest found and of every nightjar captured or recaptured was determined by compass bearing and tape distance from the nearest beacon and was then plotted on the map.

I used the technique of nightlighting (spotlight and hand net) to find and trap the nightjars during night searches, and mist nets to trap the birds on the nest by day, although initially hand nets were also used by day (Jackson, Bokmakierie, 36:86–89, 1984). Most of the nests were found as a result of trapping sitting birds at night.

To ensure individual identification, I marked the eggs and young with pink nail varnish and banded the adults with numbered bands supplied by the South African Bird Ringing Unit; the young were also banded when they reached half the adult weight.

Blinds were set up at two of the Fierynecked nests in order to observe and photograph the behavior of the birds; a light intensifying telescope (Magniscope) was used at night. One

of the nests was surrounded by a fence of wire mesh, 15 cm high and one m distant, to prevent the two young from moving away unaided before they could fly.

The nightjars in the study area suffered a considerable amount of interference at the nest as a result of routine trapping, examination, marking, weighing and measuring, with eggs, young and adults being handled freely at least once a week and as often as once or twice a day. Interference was kept to a minimum consistent with the other objectives of the study, and no attempt was made to deliberately provoke adults into transporting eggs or young away from the nest.

Results.—During the study period, covering four breeding seasons, my assistants and I captured three European Nightjars (*C. europaeus*), 79 Fierynecked (including 24 juveniles), six Freckled (*C. tristigma*) (four juveniles), 11 Mozambique (two juveniles), and eight Pennantwinged (*Macrodipteryx vexillaria*) nightjars. Most of these birds were recaptured one or more times during the course of the study (Jackson, Safring News 13:43–50, 1984). We found 60 nightjar nests (44 Fierynecked, 6 Freckled, 7 Mozambique, and 3 Pennant-winged nightjars).

At 21 nests the eggs disappeared or were deserted intact prior to hatching. Ten desertions (3 Fierynecked, 2 Freckled, 2 Mozambique, and 3 Pennantwinged nightjars) appeared to be in response to our activities. Six desertions (5 Fierynecked and one Mozambique nightjar) occurred after the birds had been sitting for several days in excess of the normal incubation period on eggs that failed to hatch. At five nests (4 Fierynecked and one Freckled nightjar) the eggs simply disappeared, as would happen if the parents had transported them to a new nest. In two of these cases, the birds concerned did nest again shortly afterwards, but in neither case was any marked egg from the old nest found in the new nest. The other three pairs (including the Freckled Nightjar) were not found nesting again in the seasons concerned.

We flushed nightjars off eggs or young on at least 338 occasions (251 Fierynecked, 60 Freckled, 19 Mozambique, 8 Pennantwinged nightjars) during our study without seeing any sign of an airlift of an egg or a chick by any parent.

On eight occasions, while in a blind, I saw nightjars moving their young by calling the young to them, 4 times by the male and 4 times by the female, including 3 during daylight. The chicks, at ages ranging from 1 to 10 days, responded immediately to the low *woot-woot-woot* . . . call of the parent by moving directly towards it, clambering over leaves, twigs, stones, grass stems, and other obstacles, sometimes up steep slopes, for distances ranging from 10 cm to 10 m. On two occasions when a fence prevented them from reaching the adult, the adult eventually flew into the fenced enclosure to join the chicks. At no stage were the adults seen to make any effort to airlift the chicks out of the enclosure, and the chicks remained confined until they could fly out at age 14 days.

My only observation of egg carrying concerned a pair of Fierynecked Nightjars nesting in a eucalyptus plantation on Retreat Farm (17°55′S, 31°03′E), Harare, Zimbabwe. The nest was found on 28 September 1967 shortly after the first egg was laid and was visited regularly thereafter in an attempt to determine the incubation period. On 15 October at 17:50 when I flushed the female off the nest she appeared to be carrying an egg below her lower breast. It was easy to follow her flight with binoculars, as there was no undergrowth in the plantation. After flying about 30 m she perched on a branch 5 m above the ground, tugged at the egg with her bill, succeeded in pulling it off and then dropped it to the ground, where I recovered it. What I found was not a complete egg, but about half of the shell, which had obviously stuck to the breast feathers, as several had come away with the shell. The nest still contained one egg, and 40 cm away lay a newly-hatched chick, thrown there when the adult took off; it too seemed to have been stuck to the adult.

This incident offers a simple explanation for the behavior of the Whip-poor-will (*C. vociferus*) that Kilham (1957) observed, and a careful reading of his detailed account shows

that it is probably the correct one. That the transportation of the egg was accidental is confirmed by the fact that the bird was still carrying the same egg when Kilham again flushed it off the nest an hour later; it had not removed the egg to a place of safety. That the egg may have stuck to the ventral plumage with albumen is suggested by the fact that one of the eggs was already hatching when the bird was flushed for the first time. A similar occurrence involving a Chuck-will's-widow was observed by Rysgaard (1944), but on that occasion the egg seemed to be attached to the bird's foot rather than to the ventral plumage. When he again flushed the bird off the nest later in the day, he found a chick struggling free from the shell, again suggesting that albumen had glued the egg to the bird. Rysgaard (1944) offers another explanation: "In all probability the shell was extremely porous and fragile just prior to hatching, and the bird had accidentally imbedded its claws into the shell and was unable to release them." When van Rossem (Trans. San Diego Soc. Nat. Hist. 8:121–148, 1936) collected a Whip-poor-will off a nest containing one nearly fresh egg he noted that "stuck to the ventral plumage of the incubating female were several small pieces of shell, showing that another egg had been laid and somehow broken." When an egg hatches or breaks for some other reason there is always a danger that an egg or some shell fragments will stick to the sitting bird. Photographs by Sundin (Vår Fågelvärld 41:31, 1982) of a Little Auk (*Plautus alle*) flying and perching with an egg stuck to its belly show this very clearly.

Austin and Singer (1961) state that "Chuck-wills have also been reported to carry their young to a safer place between their thighs the way a Woodcock will." But this behavior is by no means common in the American Woodcock (*Scolopax minor*), if it occurs at all. Tuck (Can. Wildl. Serv. Monogr. Ser. 5, 1972) points out that none of the biologists who have observed and banded hundreds of American Woodcock broods has ever seen it, and adds that if it does occur in snipe or woodcock, it is probably accidental and quite unusual. Tordoff (Loon 56:81–82, 1984) discusses the evidence and concludes that American Woodcock do not intentionally transport their young; he is also skeptical of reports of egg carrying by European Woodcock (*S. rusticola*). The evidence for European Woodcock deliberately airlifting their young is much greater (Alexander, Ibis 88:12–22, 1946); however, many of the observations concerned can be explained as optical illusions created by the distraction flight of the adult bird (Lowe, Ibis 114:106–107, 1972; Glutz von Blotzheim et al., Handbuch der Vögel Mitteleuropas, Akademische Verlagsgesellschaft, Wiesbaden, W. Germany, 1977; Cramp and Simmons, eds., The Birds of the Western Palearctic, Oxford Univ. Press, Oxford, England, 1983).

Nightjars, which have short legs and a very short bill, would have great difficulty carrying young between their thighs, yet some species have been seen carrying young beneath their bodies, e.g., the Egyptian Nightjar (*C. aegyptius*) (Robin, Oiseau Revue fr. Ornithol. 39:1–7, 1969) and the Whip-poor-will (Bent, U.S. Natl. Mus. Bull. 176, 1940). As with the transportation of eggs, the simplest explanation is that the chick observed was stuck to the ventral feathers of the adult. There is no reason to suppose that the adult was deliberately carrying it to safety.

Caprimulgids moving chicks away from danger do so by first moving away themselves and then calling the chicks to them (Skutch, pp. 200–202 *in* Bent, 1940, for the Pauraque; Weller, 1958, for the Common Nighthawk; Ganier, 1964, for the Chuck-will's-widow; Raynor, 1941, for the Whip-poor-will; pers. obs. for the Fierynecked Nightjar). Several of these authors noted that the young were very mobile within a day of hatching and I can confirm this for Fierynecked, Freckled (*C. tristigma*) and Mozambique nightjars. One Fierynecked chick that I handled less than four hours after it hatched walked about strongly on the palm of my hand, climbing up a slope of about 30°. This early mobility of the chick can lead to the mistaken assumption, when it is found to have moved, that "the parent must have carried the chick" (Cunningham-van Someren, East Afr. Nat. Hist. Soc. Bull. April:63, 1971).

Conclusions.—Caprimulgids respond to undue provocation at the nest by deserting the eggs or by calling the young away. Chicks are mobile within hours of hatching and readily move unaided towards a calling adult. There is no satisfactory evidence of adults deliberately transporting eggs or young, either in the mouth or between the thighs, as is claimed in the literature. Accidental transportation occasionally occurs when an egg or chick gets stuck to the soft ventral plumage of the sitting bird, and this would seem to be the explanation for most of the documented records.

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Temperature fluctuations and nesting behavior of Rock Wrens in a high-altitude environment.—The energetics of nesting behavior in birds has been examined by many workers (Kale, Publ. Nuttall Ornithol. Club 5, 1965; Verner, Condor 67:125–139, 1965; Walsberg, Ecology 59:147–153, 1978; Vleck, Condor 83:229–237, 1981). This paper reports observations made at a nest of Rock Wrens (*Salpinctes obsoletus*) at 3800 m above sea level. The study was conducted on 19 and 20 July 1981 at the University of California White Mountain Research Station, Inyo County, California, about 350 m above timberline. The nest was situated beneath a rock of approximately 15 cm, and opened to the southwest. Summer temperatures average from 0 to 20°C, and summer precipitation averages about one cm; winds of approximately 8 km/h were frequent. During a continuous 24-h period we recorded feeding and other behavioral patterns, and simultaneously monitored nest and ambient temperatures. The nest contained a small nestling, which we estimated to have been 2–4 days old.

Methods.—Nest temperatures (Tn) were recorded with a copper-constant thermocouple taped to the roof of the rock cavity in which the nest was located (about 8 cm from the bottom of the nest depression). Ambient temperatures (Ta) were measured with a thermometer that rested at ground level in a shaded rock crevice. Both Ta and Tn were recorded every 5 min, to obtain average hourly temperature values. Daytime parental behavior (number and duration of visits to the nest, qualitative assessment of food delivered, etc.) was observed from 12:00 to 20:45 on the first day, and from 05:00 to 12:00 on the second day. We considered the two half-days of observation as a single day. Neither parent was banded and, because the species is sexually monomorphic, we can state only that one, both, or neither of the parents was at the nest at any particular time.

Results.—Tn averaged 21.8°C and Ta averaged 22.2°C for the active period of the day (05:00–20:00 h); Tn averaged 11.3°C during the inactive period (20:00–05:00 h). The combined number of parental visits for the entire day was 298; food was brought by the parents in 240 of these visits (15 visits/h). The rate of feeding in the morning followed an hourly pattern in which an hour of high feeding rates was followed by an hour of low ones (Fig. 1). This behavior may have been caused by response of the parents to satiation of the nestling (Kendeigh, Illinois Biol. Monogr. 22:1–356, 1952). The feeding rate, which declined in the afternoon, increased shortly before nightfall; this pattern is commonly observed in other species (Kluijver, Ardea 38:99–135, 1950; Kendeigh 1952; Morehouse and Brewer, Auk 85:44–54, 1958; Anderson and Anderson, Condor 62:351–369, 1960; Nolan, Ornithol. Monogr. 26, 1978).

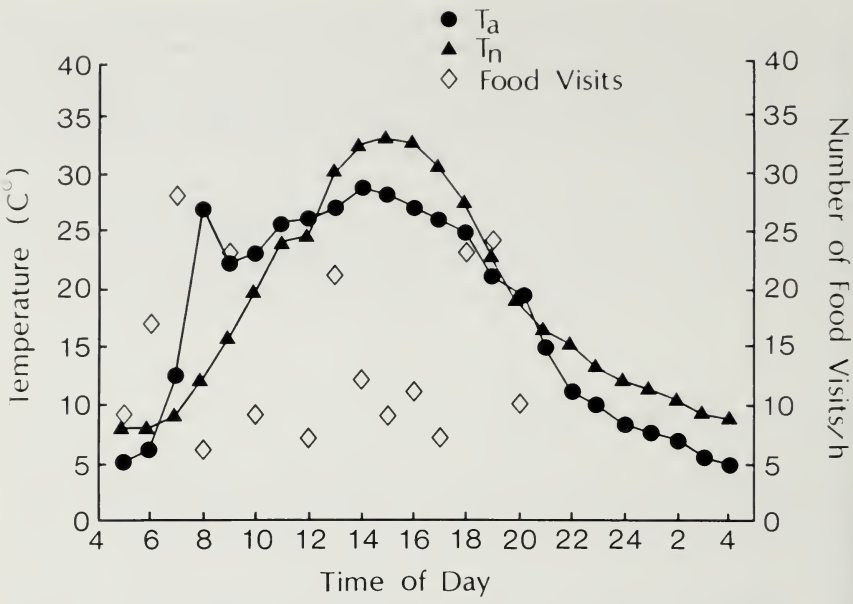

FIG. 1. Nest (Tn) and ambient (Ta) temperatures of a Rock Wren nest during a 24-h period, with the number of feeding vistits/h by both parents. Nest temperature = ▲, ambient temperature = ●, parental visits = ◇.

During the 16-h period of activity, the nestling was alone in the nest for 9 h and 15 min, or 58% of the time. The amount of time both parents spent together in the nest was usually brief (<1 min). The greatest proportion of time the nestling was alone appeared to be in the morning and early evening, presumably due to increased foraging by the parents in response to a greater demand for food at those times (Fig. 1). The nestling was alone much less during the afternoon; between 16:00 and 17:00 a parent was present for 88% of the time.

When one parent was in the nest when the second arrived, the bird already present sometimes flew out. This combined enter-exit behavior of the parents created the illusion that a single individual had entered and left the nest within a few seconds. This behavior has been reported in other species (Nolan 1978) and may function as an anti-predation mechanism.

Discussion.—Temperatures in the Rock Wren nest were usually above and more constant than Ta. Similar results have been obtained in studies of other cavity nesters (Kendeigh, Wilson Bull. 73:140–147, 1961; Mertens, Oecologia 28:1–29, 1977; McComb and Noble, J. Wildl. Manage. 45:284–289, 1981). McComb and Noble (1981) compared diurnal fluctuations in microclimates of artificial wooden nestboxes and natural tree cavities. Natural cavities (in vertical tree trunks) showed a longer temperature lag as well as decreased exposure to solar radiation relative to exposed nest boxes. Thus, by midafternoon, the temperature in the natural cavities was still below ambient temperature, whereas in nestboxes it exceeded ambient temperature. This pattern of nest temperature fluctuation is identical to that found in the Rock Wren nest in this study (Fig. 1). This suggests that the thermal inertia of typical

Rock Wren nests at White Mountain Biological Station (placed under small loose rocks) is comparable to that of exposed wooden nest boxes at lower altitudes. The combination of the horizontal orientation of the nest rock and the lack of leaf cover may have accounted for the similar temperature patterns observed in wooden nest boxes and the Rock Wren nest in this study.

The number of feeding trips to the nest (240) was higher than has been reported for most small passerines, even in larger broods (Kendeigh 1952; Anderson and Anderson 1960; Royama, Ibis 108:313–347, 1966; Nolan, 1978). As the nestling was probably not yet endothermic, it is doubtful that it was using large amounts of food for thermoregulation. The nutritional value of the insects may have been low or the parents may have eaten some of the food themselves. Further investigation is needed to compare the behavior of Rock Wrens at various altitudes to determine the effects of arctic-alpine habitat on the reproductive biology of these cavity nesting birds.

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A second brood by Canada Geese.—Canada Geese (*Branta canadensis*) normally attempt one nest each year. If the first nesting attempt fails early in the nesting cycle, renesting often occurs (Craighead and Craighead, J. Wildl. Manage. 13:51–64, 1949; Kossack, Am. Midl. Nat. 43:627–649, 1950; others summarized by Bellrose, Ducks, Geese and Swans of North America, 3rd ed., Stackpole, Harrisburg, Pennsylvania, 1976). At Trimble Wildlife Area, Missouri, female geese often made as many as two renesting attempts following failures, but only if the nest was destroyed before the fifth day of incubation (Brakhage, J. Wildl. Manage. 29:751–771, 1965). Renesting was common at Marshy Point, Manitoba, where 92% of the pairs that lost clutches during laying made a second attempt. Renesting did not occur, however, if the first nest was destroyed after the second day of incubation (Cooper, Wildl. Monogr. 61, 1978). Renesting occurred only up to the tenth day of incubation at Dog Lake, Manitoba (Klopman, Wilson Bull. 70:168–183, 1958). To my knowledge, additional nesting attempts have not been reported for Canada Geese when nests were destroyed late in incubation or at hatching, and second broods in Canada Geese have not been reported previously.

In Clinton County, northwestern Missouri, an individually marked pair (neck-collared female and leg-banded male) of resident Canada Geese (*B. c. maxima*) successfully hatched two clutches in the spring of 1983. The pair nested in an elevated man-made nesting structure in a farm pond. The female was at least 5 years old, and the male at least 3 years old. In both nests, only one egg hatched. The female began laying the first clutch of 10 eggs on 8 March 1983. One egg hatched on 22 April 1983, and the nesting pair left the pond with the gosling. The same pair returned to the nest pond without the gosling in early May. The female laid the first of 9 eggs in a new clutch on 16 May 1983. One of these eggs hatched

on 26 June 1983. At that time, most other goslings produced in the vicinity were nearing flight stage. The fates of adults and the gosling of the second clutch were unknown. The first egg was laid in the second nest 24 days after the first gosling hatched.

Sixteen of the 17 unhatched eggs (9 in the first nest and 8 in the second) were in advanced stages of decomposition. Fertility in these eggs could not be verified. One egg in the second clutch contained an embryo that died after 21 days of development (Cooper and Batt, J. Wildl. Manage. 36:1267–1270, 1972). Although both clutches were unusually large, other geese probably did not contribute eggs to the clutches. No other geese were observed in the immediate vicinity of the nest pond, and the closest nesting pair was 1.5 km away.

Most wild anatids are not normally double-brooded (Weller, pp. 35–79 *in* The Waterfowl of the World, Vol. 4, J. Delacour, ed., Country Life Ltd., London, England, 1964). Renesting following loss of broods by Northern Pintails (*Anas acuta*) has been reported in southern Manitoba (Sowls, Prairie Ducks, University of Nebraska Press, Lincoln, Nebraska, 1955). Three percent of nesting female Wood Ducks (*Aix sponsa*) have second broods in southeastern Missouri (Fredrickson and Hansen, J. Wildl. Manage. 47:320–326, 1983). Food supply for the nesting female Wood Ducks and the length of the season are key factors affecting the occurrence of double broods (Fredrickson and Hansen 1983). The instance of double-brooding in the resident flock of Canada Geese near Trimble, Missouri, may have been related to the potentially prolonged nesting season (usually beginning in mid-March and running, in this case, through to the end of June), the absence of the energetic cost of spring migration, or the availability of abundant nutrient and energy resources in the surrounding farmland.

I thank T. S. Baskett and L. H. Fredrickson for reviewing this manuscript. The observations reported here were made during an investigation of Canada Goose production funded by the Missouri Department of Conservation (Pittman-Robertson W-13-R) and the Missouri Cooperative Wildlife Research Unit. This is a contribution from the Missouri Agricultural Experiment Station, Project 184, Journal Series No. 9657.—David H. Brakhage, *School of Forestry, Fisheries and Wildlife, Univ. Missouri, Columbia, Missouri 65211.* (Present address: *Florida Game and Fresh Water Fish Commission, 3991 SE 27th Court, Okeechobee, Florida 33474.*) *Accepted 30 Jan. 1985.*

Wilson Bull., 97(3), 1985, pp. 388–389

A four-egg clutch of the Mountain Plover.—Nests of Mountain Plovers (*Charadrius montanus*) typically contain 2–3 eggs, which are relatively uniform in size and color. Graul (pers. obs.) has examined nearly 200 nests, only one of which contained four eggs. On 7 May 1983 we found an additional four-egg clutch approximately 2 km south of Keota, Weld County, Colorado.

Three of the four eggs were relatively uniform in size and color. However, one egg weighed 3.0–3.5 g less than the others, a difference of 18–20%, and lacked the same ground color and markings. Whether eggs of individual plovers are distinctive has not been demonstrated, but Vaisanen (Ornis Fenn. 49:25–44, 1972) found that egg variation among individual waders remained nearly the same within a breeding season and from year to year.

Walters and Walters (Ibis 122:505–509, 1980) reported cooperative breeding in otherwise monogamous lapwings whose nest contained eggs differing in coloration. Alternatively, nests containing eggs of different sizes and colors may be the result of intraspecific parasitism. Sordahl (*in* Yom-Tov, Biol. Rev. 55:93–108, 1980) indicated possible intraspecific para-

sitism in the American Avocet (*Recurvirostra americana*) and the Black-necked Silt (*Himantopus mexicanus*), but his observations were not conclusive.

Graul's interpretation of the Mountain Plover's mating system (Living Bird 12:69–94, 1973) was substantiated by observations of marked birds involved with a specific nest, but he did not consider additional individuals being involved with the same nest. Future studies of this species should therefore direct attention to the possibility that clutches containing distinct eggs may be the result of two females laying in the same nest.

Acknowledgments.—J. P. Myers and L. W. Oring offered helpful comments on the manuscript.—Michael J. Hamas, *Dept. Biology, Central Michigan Univ., Mt. Pleasant, Michigan 48859,* and Walter D. Graul, *Colorado Division of Wildlife, 317 W. Prospect, Ft. Collins, Colorado 80526.* *Accepted 25 Mar. 1985.*

Wilson Bull., 97(3), 1985, pp. 389–390

Territorial behavior of American Crows.—Territoriality in American Crows (*Corvus brachyrhynchos*) is mentioned by Knopf and Knopf (Wilson Bull. 95:153–155, 1983). Chamberlain and Cornwell (Auk: 613–634, 1971) and Richards and Thompson (Behaviour 64: 184–203, 1978) have described certain vocalizations of American Crows, but as they have not provided territorial or other precise contexts, their work is difficult to interpret. Verbeek et al. (Ibis 123:183–189, 1981) and Butler et al. (Wilson Bull. 96:408–418, 1984) have described territoriality in the Northwestern Crow (*C. caurinus*). This note describes displays, chases, and other patterns of territorial behavior in American Crows in New Hampshire. I watched territorial encounters (N = 45) between two groups of unmarked crows from farm buildings that faced over 30 ha of fields. The two groups were divided by a territorial boundary that ran from a wooded area on the W to buildings on the E, a distance of 150 m. The boundary had no special features other than two dead American elms (*Ulmus americana*) that were frequently used for perching by the groups of crows prior to making attacks. In 1983 the boundary was 60 m to the south, its only markers in fields being the positions of the rival crows facing each other. I called the crows N of the boundary the N crows and those to the S, S crows. In November and December of 1982 there were 3 N and 3 S crows, in the summer of 1983, 4 N and 10 S crows, and in November and December 1983, 3 N and 5 S crows. These numbers were constant once seasonally established, except for scattered days in November and December, when one or two individuals were not seen. Daily counts were facilitated by there being no other crows at the farm and by the members of each group moving about more or less together. I visited the farm every day, with few exceptions, from 1 September until the end of December in 1982 and from 1 July to 30 December in 1983, and watched crows for about 500 h.

Although no two encounters were exactly alike, a number of behavioral patterns were observed repeatedly. *Cawing* (N = 43) consisted of many sharp, brief *caws* corresponding to what Good (Ph.D. diss., The Ohio State Univ., Columbus, Ohio, 1952) designates as a "warning" and Chamberlain and Cornwell (1971) call "simple scolding" calls. The crows of both groups *cawed* when flying toward each other, especially early in the morning. If one group alighted in the field and the other in trees, the latter did the most *cawing. Caws* at high intensity were acompanied by *cawing* displays in which the whole body became involved, with the wings moving out at the "shoulders," the tail spreading, and the head bowing down, then swinging up. Walking displays (N = 17) consisted of rival crows walking toward each other. In a representative encounter on 20 August 1983, the S crows alighted

20–30 m to their side of the boundary, and the N crows—the more aggressive group—did the same. The two groups then walked slowly toward each other for 10–15 min, foraging as they went. When they were about 15 m apart, the N crows took wing and swooped down within 15–20 cm of the leading S crow, which sometimes squatted on the grass with wings outspread. When the N crows returned to the ground, the two groups turned to walk back the way they had come. Intrusions (N = 5) were seen in the fall of 1983 when an N crow alighted 12–16 m inside the S group's territory while the two other N birds remained at the boundary. The single N crow clashed with the nearest S crow. On 11 and 15 December the N crows occupied the vicinity of the boundary with similar positions for 10–20 min at the start of the day, before the S crows appeared.

Other behavioral patterns included "aerial melees" (N = 17), "bunching" (N = 5), and "pursuits" (N = 5). Aerial melees were spectacular, with all members of both groups swirling into the air for 3–4 sec, with some of them swooping on others. On 19 November 1982, the N and S crows, flying from perches on the elms, had five such encounters in 12 min. When about to fly against opponents, crows of either group sometimes flew to within 15–30 cm of each other. On 8 December 1982 the 3 S crows, after grouping in this manner, repeatedly dove on the N crows, driving them 250 m north of the boundary. This was one of the few encounters in which the S crows initiated the interaction. Territorial behavior also included slow, circular flights (N = 11), in which crows of one group circled a short way over the border, then returned to their own territory, and tree-top sitting (N = 17), in which the crows climbed to the top of the dead elms or other bare trees during the territorial encounters. Displacement activities (Terres, Encyclopedia of North American Birds. Alfred A. Knopf, New York, New York, 1980), which I saw only twice, consisted of exaggerated bill-wiping and bark-pecking. "Wing-tail flicking," which in my experience is sometimes a sign of readiness to attack (Kilham, Fla. Field Nat. 13:25–48, 1985), was seen during most encounters.

Good (1952) found no indications of territoriality, except close to nests, at any season among American Crows in Ohio. Territorial behavior, however, can be missed if an observer does not happen upon a section of boundary where neighboring groups meet. I have observed encounters along boundaries between groups of cooperatively breeding crows (Kilham, J. Field Ornithol. 55:349–356, 1984) in Florida during the breeding season, as well as among crows in New Hampshire in summer, fall, and winter. Other species of *Corvus* defending territories include the Carrion Crow (*C. corone*) (J. K. Charles, Ph.D. diss, Aberdeen Univ., Aberdeen, Scotland, 1972), the Jungle Crow (*C. macrorhynchos*) (Kuroda, Misc. Rep. Yamashina Inst. Ornithol. 44:1–34, 1975), and the Black Crow (*C. capensis*) (Skead, Ibis 94: 434–451, 1952). Tree-top sitting as a form of territorial behavior is well developed in Black Magpies (*Pica pica*) (Moller, Ornis Scand. 13:94–100, 1982).—LAWRENCE KILHAM, *Dept. Microbiology, Dartmouth Medical School, Hanover, New Hampshire 03755.* *Accepted 4 Mar. 1985.*

Wilson Bull., 97(3), 1985, pp. 390–392

The status of the Sooty Storm-Petrel in Hawaii.—The total U.S. population of the Sooty Storm-Petrel (*Oceanodroma tristrami*) is estimated to be less than 10,000, and the species has been designated a "sensitive species" by the U.S. Fish and Wildlife Service (USFWS Regional Planning Manual, 1979). The species has a narrow breeding range limited to North Pacific islands, and in Hawaii it breeds on French Frigate Shoals (Amerson, Atoll Res. Bull.

150, 1971), Laysan Island (Ely and Clapp, Atoll Res. Bull. 171, 1973), and Pearl and Hermes Reef (Amerson et al., Atoll Res. Bull. 174, 1974). It has been suspected of breeding on Nihoa Island (Clapp et al., Atoll Res. Bull. 207, 1977), Necker Island (Clapp and Kridler, Atoll Res. Bull. 206, 1977), and Lisianski Island (Clapp and Wirtz, Atoll Res. Bull. 186, 1972). King (Smithson. Inst. Bull., 1967) lists the Volcano Islands and the Southern Izu Islands of Japan as breeding sites, along with possibly the Bonin (Ogasawara) Islands. Hasegawa (Yamashina Inst. Ornithol. 10:178–184, 1978) commented that the population "appears to have greatly decreased recently" at the Izu Islands. The limited breeding range of the species suggests that the population center is in Hawaii. Here we report a summary of our field observations of this species from 1978–1983.

Distribution.—We conducted a survey of Nihoa Island from 31 January to 22 February 1981 at which time eggs, and chicks in various stages of growth, were found. Birds were heard calling from burrows in loose rock piles in valleys and in soil at the summit of the island. We estimated the number of calling pairs from these colonies; then, based on the amount of similar habitat, we estimated that Nihoa might support approximately 2000–3000 breeding pairs. In 1981 and 1983, several specimens were collected. They were identified and deposited at the U.S. National Museum of Natural History in Washington, D.C. (USNM 507668) and at the B. P. Bishop Museum in Honolulu, Hawaii (BPBM 1983.338). We observed a chick, almost fully-feathered with some down remaining on its belly, on 21 May 1979 on Necker Island confirming that Sooty Storm-Petrels breed there. In June 1982, a mummified chick of the same age was collected and deposited in the Bishop Museum. Further nocturnal surveys are needed during the winter to determine the size of the population on Necker Island. East and Whale-Skate islands within French Frigate Shoals are breeding locations for as many as 10–15 pairs. Burrows of Sooty Storm-Petrels have been found on Whale-Skate Island at the base of albatross nest mounds (Eilerts, pers. comm.).

We estimated that between 500 and 2500 pairs may breed on Laysan Island in several scattered colonies around a hypersaline lake. Burrows were found at night by locating calling birds. Daytime surveys determined burrow occupancy and vegetation associations. Burrows were found in sandy loam substrate beneath beach morning glory (*Ipomoea pes-caprae*) and in piles of guano rock. The lack of intensive winter field work rendered such estimates imprecise. Mummified Sooty Storm-Petrels were collected on Lisianski Island in 1979, 1980, and 1982. Burrow searches for Bonin Petrels (*Pterodroma hypoleuca*) were conducted in May 1981. During that search, no Sooty Storm-Petrels were found. Consequently, we concluded that storm-petrels may breed there but that the population is small. Based primarily on information reported by Amerson et al. (1974), we estimated that 300 to 500 pairs breed on Pearl and Hermes Reef. Visits to this atoll on 10–11 May 1979 failed to reveal significant numbers of young. Burrows were found under clumps of beach grass (*Eragrostis variabilis*) and in coral rubble. Despite numerous trips to Midway Atoll between 1979 and 1983, we never observed any evidence of breeding Sooty Storm-Petrels. However, Grant ('Elepaio 43:1, 1982) found a dead adult male with enlarged testes (USNM 577154) and an unsexed adult (USNM 598525) in 1981. No nests were found. The introduced black rat (*Rattus rattus*), which has greatly reduced the nesting success of Bonin Petrels, would probably render the storm-petrel efforts unsuccessful. There have been no recent observations of Sooty Storm-Petrels nesting on Kure Atoll, but it is possible that a few pairs occur there despite the presence of Polynesian rats (*R. exulans*). Some nesting occurred there in the 1960s while rats were present (Woodward, Atoll Res. Bull. 164, 1972).

Breeding phenology.—Crossin (Smithson. Contrib. Zool. 158:154–205, 1974) acknowledged that data on Sooty Storm-Petrels in the Northwestern Hawaiian Islands were inadequate to obtain a clear picture of the breeding cycle, but that storm-petrels were present on the breeding grounds from "at least October to May and that December and January

are the peak egg-laying months." We agree with these findings and add that it is unlikely that many adults are on the breeding grounds in October, April, or May. On 5 November 1980, we could not find any birds during a fairly thorough one-day search of Nihoa, nor did we see any birds offshore. On Laysan, birds were vocalizing in burrows, but no eggs could be found on 16 November 1980. On 26 January 1981, eggs were being incubated on Laysan Island, but no young were found. In February 1981, every stage of development between eggs and fully-feathered chicks was found on Nihoa. Our surveys throughout 1978–1983 indicate that most adults and young are gone from the breeding islands by mid-May.

Morphometrics.—Adult Laysan Island birds ($\bar{x}$ = 93.8 g, SD = 9.8, range = 79–108.5, N = 32) weighed significantly more than adult Nihoa birds ($\bar{x}$ = 86.2 g, SD = 6.0, range = 74–94, N = 23) (ANOVA, $P \leq 0.01$) in January and February. Adult weights on Laysan in April and May averaged 83.6 g (range = 66–105, N = 61). The differences in weight may reflect seasonal and spatial food availability. The following mean measurements are from Nihoa: culmen length 1.86 cm (SD = 0.13, range = 1.64–2.29, N = 23); culmen width 0.94 cm (SD = 0.08, range = 0.79–1.06, N = 13); tarsi 3.03 cm (SD = 0.16, range = 2.71–3.40, N = 23) and wing length 11 cm (SD = 0.64, range = 17.5–19.5, N = 11). The single egg is immaculate white, not with spots as reported by Peterson (1961). Egg measurements were made from 9 eggs on Laysan Island. The mean length was 3.91 cm (SD = 0.11, range = 3.70–4.14) and the mean breadth was 2.87 cm (SD = 0.06, range = 2.77–2.96). Two eggs were measured in Nihoa. The mean length was 3.78 cm (SD = 0.18, range = 2.67–2.92). The egg volumes were calculated according to Stonehouse (Ibis 103:474–479, 1963) to be 16.04 cm^3 and 15.06 cm^3 respectively (ANOVA, $P > 0.01$).

Conservation.—The Sooty Storm-Petrel population is now known to be greater than previously suspected in the Northwestern Hawaiian Islands with the confirmed presence of a large colony on Nihoa Island. Nowhere, however, is this ground-nesting species common. The accidental introduction of rats or cats onto breeding islands could be devastating. Rats were responsible for a population decline at the Izu Islands, Japan (Hasegawa 1978). Additional research is necessary during the winter breeding season to determine the actual size of the colonies. To be effective, thorough surveys require the use of tape recordings of the Sooty Storm-Petrel call to determine the occurrence of birds in their deep burrows. A more accurate status assessment throughout its range will help determine what conservation measures, if any, are needed.

Acknowledgments.—We are grateful to the captain and crew of the NOAA Ship R/V *Townsend Cromwell* for their support of our field studies. A. Newman, E. Knudtson, B. Flint, J. Andre, R. Schulmeister, S. Schulmeister, and R. Ittner made observations that were used in this report. We thank R. B. Clapp and S. L. Olson for indentifying specimens. We also thank the U.S. Fish and Wildlife Service for their support.—MARK J. RAUZON, *P.O. Box 4423, Berkeley, California 94704;* CRAIG S. HARRISON, *46-024 Puulena, #614, Kaneohe, Hawaii 96744;* AND SHEILA CONANT, *Dept. General Science, Univ. Hawaii, Honolulu, Hawaii 96822.* *Accepted 1 Feb. 1985.*

Wilson Bull., 97(3), 1985, pp. 392–395

Vocal imitation in a captive Purple Martin.—Kroodsma and Baylis (pp. 311–389 *in* Acoustic Communication in Birds, Vol. 2, D. E. Kroodsma and E. H. Miller, eds., Academic Press, New York, New York, 1982) list the Barn Swallow (*Hirundo rustica*) as the sole representative of the Hirundinidae known to show vocal imitation. Here, I report vocal

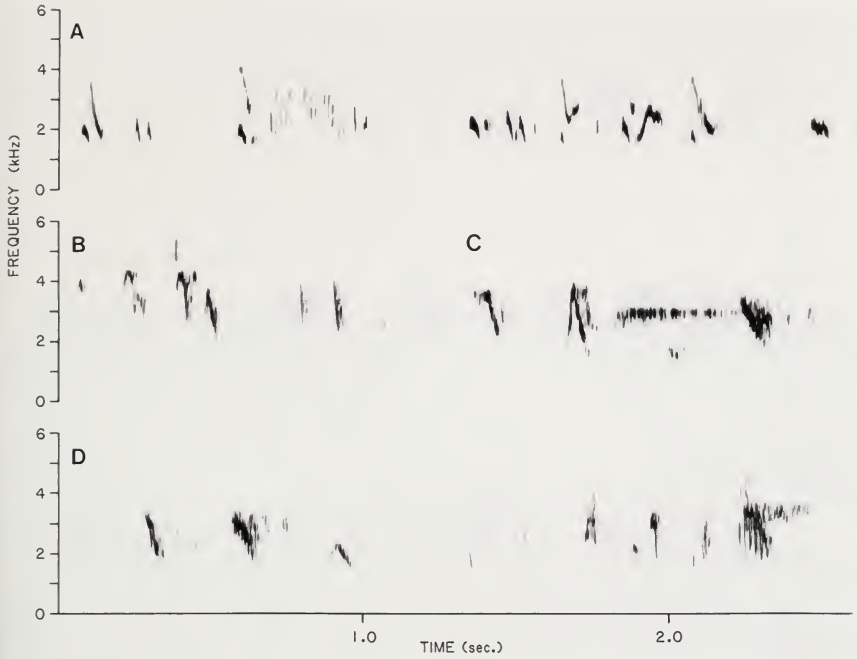

FIG. 1. Wide-band spectrograms of sounds of a captive male Purple Martin isolated as a nestling from visual or auditory contact with wild martins. (A) Sound recorded before exposure to heterospecific songs in the National Zoo's Bird Exhibit Building. (B) and (C) Imitations of a Golden-fronted Leafbird. (D) Imitation of a Red-crested Cardinal.

mimicry in a captive Purple Martin (*Progne subis*). In July 1980, six nestling martins were taken from a colony at 8–10 days of age and raised in the basement of the Bird Exhibit Building, National Zoological Park, Washington, D.C. They had no further visual or auditory exposure to wild martins, and were released into a large indoor "tropical rainforest" exhibit (31.7 × 39 × 40 m) in January 1981. Two survived until spring 1981, and one male remains, having been alone from September 1981 until an albino martin was introduced in August 1983.

The male martin shared the exhibit with one pair each of two exceptionally vocal and mimetic species, the Golden-fronted Leafbird (*Chloropsis aurifrons*) and the Red-crested Cardinal (*Paroaria cornonata*), both of whose loud songs it incorporated into loud, variable, and lengthy (>30-min) songs of its own. The subsong of the survivor recorded before it was released into the exhibit resembled Purple Martin sounds more than recordings made after the bird had experienced heterospecific sounds (Fig. 1). Loud songs were heard every month but were most noticeable from January through August, when the bird was probably in breeding condition. The martin uttered call notes, including a liquid *cher* and *zweet* in flight, and a harsh *zwrack* in aggressive encounters with heterospecifics in the exhibit that were identical to my ear to the calls of free-ranging Purple Martins (cf. Brown, Condor 86:433–442, 1984.) Sound spectrograms of the imitative songs are unlike any given by free-ranging martins (cf. Brown 1984). As elements from sounds of two heterospecifics were incorporated in these sounds, I interpret this vocal appropriation as evidence of song learning.

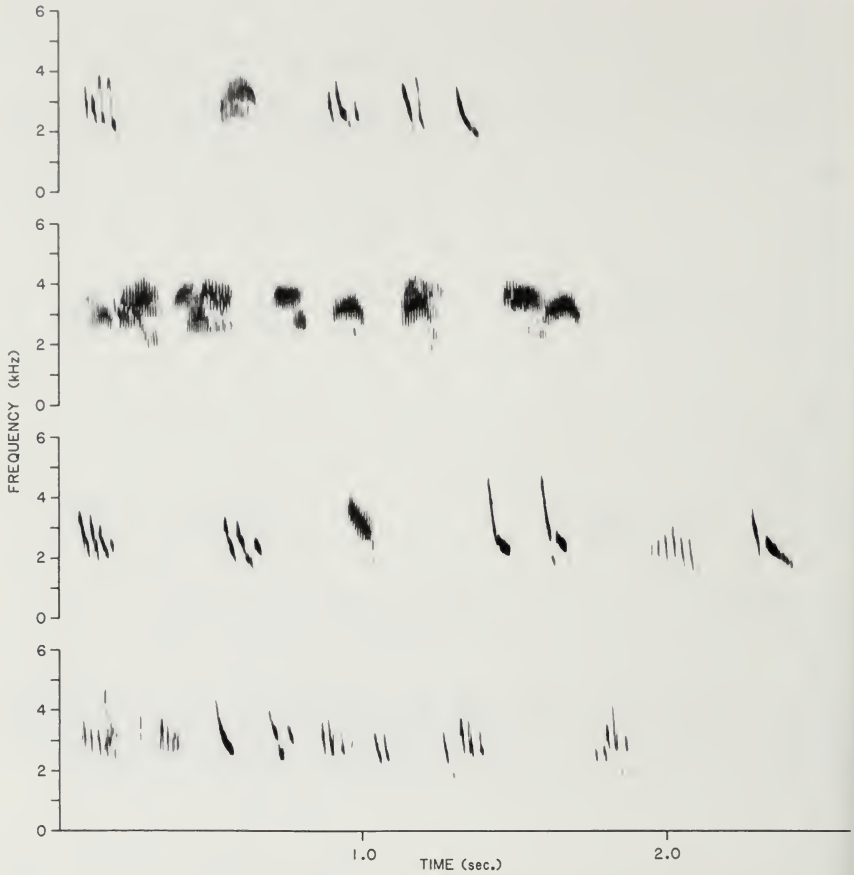

FIG. 2. Wide-band sound spectrograms of dawnsong of four male Purple Martins from the same breeding colony (Severna Park, Maryland). Note the distinctive syllables and cadences for each male's song.

Wild martins have two stereotyped songs, one given mainly during daylight hours at or near the nest cavity ("croak" song, Brown 1984) and a dawnsong consisting of a continuous (lasting from 04:15 to 05:30, late May to mid-June in Maryland, pers. obs.) rhythmic series of separate *chirp, chick,* and *chiree* sounds given in high circling flight during dark, predawn periods and occasionally while perched on the breeding box (Fig. 2). Each male at my study colony (pers. obs.) had an individually distinctive dawnsong, both with regard to cadence and note structure (Fig. 2).

I suggest that the captive male's mimicked song is a homologue of dawnsong found in free-ranging males. The dawn song of the captive male had a distinctive cadence, and was sung away from a nest site. Also, before exposure to heterospecific song, the isolated martin's dawn song strongly resembled that of wild martins in both cadence and in the structure of some syllables (Fig. 1A). The Barn Swallow, the other known hirundine vocal imitator, also has a distinctive dawnsong (pers. obs.). The function of dawnsongs in swallows, which

presumably do not defend feeding territories, remains unknown. Dawnsinging is performed by mated male martins with well-established nests (pers. obs.).—Eugene S. Morton, *National Zoological Park, Smithsonian Institution, Washington, D.C. 20008. Accepted 12 Apr. 1985.*

Wilson Bull., 97(3), 1985, p. 395

Observations of a Tufted Titmouse and a Cattle Egret associating with a black bear.—On 2 May 1980, in a bottomland hardwood forest in eastern Arkansas, I located a yearling male black bear (*Ursus americanus*) and his radio-collared mother in a water hickory tree (*Carya aquatica*) in one m deep floodwater. While preparing to tranquilize the juvenile bear, I observed a Tufted Titmouse (*Parus bicolor*) jumping about the bear's back and rump pecking at its fur. After a few minutes, I noticed that the titmouse was collecting hair in its beak, and carrying it from the site. During a period of approximately 30 min, an adult titmouse, presumably the same bird, returned to the bear twice to repeat this behavior. The third hair-gathering episode was interrupted, however, as I approached the bear.

It is likely that the titmouse was using the collected hair in its nest. The incident occurred during the nesting period of the Tufted Titmouse in this region (Douglas and Neal, Arkansas Birds: Their Distribution and Abundance, Univ. Arkansas Press, Fayetteville, Arkansas, in press), and this species has been reported to use the hair of a variety of mammals to line its nest (Bent, U.S. Natl. Mus. Bull. No. 191, 1946; Pielou, Ph.D. diss., Michigan State Univ., Lansing, Michigan, 1957). The Tufted Titmouse has been observed collecting hair from living mammals including red squirrel (*Tamiasciurus hudsonicus*), woodchuck (*Marmota monax*), and human (*Homo sapiens*) (Bent 1946), and opossum (*Didelphis marsupialis*) (Goertz, Wilson Bull. 74:189–190, 1962), but not black bear.

In the same forest on 13 September 1980, I saw a radio-collared adult male black bear wading in a shallow lake with a Cattle Egret (*Bubulcus ibis*) perched on its back. Cattle Egrets have been reported feeding alongside and atop a number of African ungulates including elephant (*Loxodonta africans*), rhinoceros (*Diceros bicornis*), and hippopotamus (*Hippopotamus amphibus*), where they prey upon insects stirred up by these mammals and, possibly, ectoparasites (Pitman, Bull. Br. Ornithol. Club 82:100–101, 1962; Brown, The Birds of Africa, Vol. I, Academic Press, London, England, 1982).—Tommy R. Smith, *Graduate Program in Ecology, and Dept. Forestry, Wildlife and Fisheries, Univ. Tennessee, P.O. Box 1071, Knoxville, Tennessee 37916-1071. Accepted 8 Apr. 1985.*

Wilson Bull., 97(3), 1985, pp. 395–396

Abnormal yellow eye ring on a Tropical Kingbird.—Abnormal yellow plumage occurs rarely among wild birds, and is generally known as xanthochroism (e.g., Pettingill, Ornithology in Laboratory and Field, 4th ed., Burgess Publ. Co., Minneapolis, Minnesota, 1970: 193; Van Tyne and Berger, Fundamentals of Ornithology, 2nd ed., Wiley and Sons, New York, New York, 1976:161; Terres, The Audubon Society Encyclopedia of North American

Birds, Alfred A. Knopf, New York, New York 1980:98; Welty, The Life of Birds, 3rd ed., Saunders College Publ., Philadelphia, Pennsylvania, 1982:56). Hailman (Fla. Field Nat. 12: 36–38, 1984), however, has pointed out that the term "xanthochroism" has several meanings, and that its use should be avoided in descriptions. Both Buckley (pp. 21–110 *in* Diseases of Cage and Aviary Birds, M. Petrak, ed., 2nd ed., Lea and Febiger, Philadelphia, Pennsylvania, 1982) and Hailman (1984) recommend abandoning many of the traditional terms for avian coloration because of their ambiguity, and emphasize the importance of reporting abnormally colored birds in order to gain a greater understanding of the pigmental and genetic bases of avian coloration.

On 18 Aug. 1984 we observed two adult Tropical Kingbirds (*Tyrannus melancholicus*) near the top of a dead tree near Hotel Jaguar, several km downstream from Puerto Misahualli, along the Rio Napo River in eastern Ecuador. One of the birds possessed a complete bright yellow eye ring about 2 mm wide on the right side of the head, and normal plumage on the left side. We observed the bird in good light through 7 × 42 binoculars for 10 min from a distance of 40 m. The three of us agreed the eye ring color was bright yellow, about the same shade as the feathers on the belly of the bird. Other than the abnormal eye ring, the bird appeared normal. Unfortunately, the birds flew away before we were able to approach close enough to take photographs.

In adult Tropical Kingbirds carotenoid and eumelanin pigments are responsible for the colors of the underparts and upperparts respectively. Apparently the yellow eye ring resulted from a mutation in which the eumelanin pigments were absent, thus exposing the carotenoid pigments. Such mutations are examples of non-eumelanic schizochroism, and have been described in several species of birds (Harrison, Bull. Br. Ornithol. Club 83:90–96, 1963; Bird-Banding 37:121, 1966; Schnell and Caldwell, Auk 83:667–668, 1966; Braun et al., Southwest. Nat. 24:391–393, 1979; Curtis, West. Birds 12:185, 1981), but not in the family Tyrannidae. This mosaic individual could have resulted either from a somatic mutation during development, or from the inactivation or loss of one allele in a heterozygote by heterochromatinization or nondisjunction.

Acknowledgments.—For their helpful comments in preparing this note we thank K. L. Bildstein, G. L. Bradley, E. H. Burt, Jr., J. P. Hailman, and W. K. Hayes. We also thank L. E. Harris, Jr., for leadership during our excursion into the Rio Napo region.—Floyd E. Hayes, William S. Baker, and Kent R. Beaman, *Dept. Biology, Loma Linda Univ., Riverside, California 92515.* *Accepted 20 Mar. 1985.*

Wilson Bull., 97(3), 1985, pp. 397–404

ORNITHOLOGICAL LITERATURE

THE BIRDS OF CHINA. By Rodolphe Meyer de Schauensee. Smithsonian Institution Press, Washington, D.C., 1984:602 pp., 512 species illustrated in 38 color plates (23 by John Henry Dick, 11 by John A. Gwynne, Jr., and 4 by H. Wayne Trimm); 39 black-and-white wash drawings in habitat by Michel Kleinbaum. $45.00 (hard cover), $29.95 (paper).—This book is a descriptive catalogue of 1200 species of birds (the author says 1195) belonging to 88 families known for China, including the islands of Taiwan and Hainan. The book starts with a foreword by S. Dillon Ripley, an explanatory first chapter, the color plates, and then the text with the wash drawings interspersed. The first chapter also contains an introduction to the geography and to the history of ornithology in China. The text is followed by a bibliography, a list of bird names used that differ from those used in Cheng Tso-Hsin's "Distributional List of Chinese Birds" (Science Publ. Co., Peking, China, 1976), a checklist of the birds of China, and indices of English and Latin bird names. The bulk of the text contains a fairly detailed description of the adult male of each species. When different, females, immatures, color phases, and subspecies are also described. Morphological descriptions are followed by the range of each species (and subspecies if different), usually a one-sentence description of habitat, and occasionally a brief comment on habits or voice.

This ambitious work marks a significant contribution to the ornithology of China, as it is the first book in English covering all the birds of that country. The strength of the book lies in the detailed morphological descriptions of the birds, 43% of which are backed by good color illustrations. Each illustration and perhaps many species descriptions are based on only one specimen. The black-and-white wash drawings are a welcome addition in a book providing scarcely any information on habitat, ecology, or behavior as compared with "Les oiseaux de Chine" (Etchecopar and Hue, Les editions du Pacifique, Papeete, Tahiti, 1978).

The range description for each species and subspecies is detailed and generally accurate (although four species of warblers resident in Taiwan are not listed [i.e., *Prinia polychroa, Abroscopus albogularis, Cisticola juncidis,* and *C. exilis*]). People who are not intimately familiar with the geography of China, however, will not easily visualize the ranges based on the text alone. Unfortunately, the endpaper maps of China and Asia are printed on very dark paper, making them hard to read and greatly reducing their utility as a supplement to the text. The inclusion of simple, shaded range maps common to many bird books would have greatly enhanced the text. Local endemism is never specifically denoted, although it usually can be inferred from the range description (one unclear exception is the Formosan Barwing [*Actinodura morrisoniana*], which is endemic to Taiwan but not found on the mainland as implied in the text). Nor is status given to indicate whether a species is common or rare.

The color plates are of good quality, although in five of them birds are not drawn to scale, as the author notes. There are some numbering mistakes and irregularities in the plates. The two trogons (*Harpactes* spp.) on Plate 12, and the Ruddy Kingfisher (*Halcyon coromanda*) and Stork-billed Kingfisher (*Pelargopsis capensis*) on Plate 13 are reversed. The numbering system on some of the plates separates normal grouping of birds. On Plate 18, for example, leafbirds (Irenidae) and the Grandala (*Grandala coelicolor,* Turdidae) come in the middle of bulbuls (Pycnonotidae). Elsewhere, the numbering divorces the male and female of the same species as if they were unrelated, although they are drawn side by side (e.g., Plates 18 and 35). Similarly, eight species of laughingthrushes (*Garrulax* spp.) appear with the broadbills (Eurylaimidae) and the pittas (Pittidae) on Plate 16, while seven other laughingthrushes follow 10 families later in their proper taxonomic position (Plate 22).

The author warns that this is not a "typical field guide." Nevertheless, it is really the only book on the market that can presently meet this need. Cheng's distribution list is in Chinese and without illustrations. Etchecopar and Hue's two huge volumes are beyond field size. This book is still manageable and the illustrations, therefore, beg for those Peterson-like pointers denoting major field marks, particularly among similar-looking species. Although these field marks are italicized in the text, they take time to locate, read through, and then compare with the illustrations. Of course, one wishes for color illustrations of the remaining 57% of the species in the same volume, instead of having to refer to other "standard references on birds of this avifauna" as suggested by the author. Also, it would have been helpful if those "easily found" standard references had been identified specifically in the bibliography.

Some significant references dealing with China's avifauna appear to have been overlooked or omitted from the bibliography. None of Robert Swinhoe's or Nagamichi Kuroda's publications are listed. Important early publications by La Touche, Takatsukasa, and others are omitted. Examples of more recent relevant publications are Blackshaw, Quart. J. Taiwan Museum 31:297–316, 1978; Marshall, AOU Ornithol. Monogr. 25, 1978; Mees, Zoologische Mededelignen 1970:285–304 and 1977:243–264; and Severinghaus, Bull. Br. Ornithol. Club 97:103–104, 1977.

Overall, this book is essential for anyone making an ornithologial field trip to China. It is a valuable addition to any ornithological library, and will be of use to people interested in the birds of China.—Lucia Liu Severinghaus.

Censo de Aves en el Mediterraneo/Bird Census and Mediterranean Landscape. By F. J. Purroy (ed.). Proceedings of the VII International Conference on Bird Census, I[nternational] B[ird] C[ensus] C[ommittee], León, Espana, 8–12 IX 1981. Universidad de León, 1983:196 pp., many maps and text figs. $4.50 (postpaid). Available from: Prof. F. J. Purroy Iraizoz, Catedrático de Zoologia (Vertebrados), Universidad de León, León, Spain.—The 35 papers included here were given at the biennial meeting of the IBCC in 1981. The papers are in English or Spanish, with a summary in the other language. The title is somewhat misleading as only a fraction of the papers deal with work in the Mediterranean region. Other papers go as far afield as northern Europe and the United States. While some of the papers present the results of individual studies, most are methodological in nature. Another group of papers reports on the progress of various Atlas projects now dominating the international ornithological scene.

All persons interested in bird censusing will be interested in the papers that present comparisons among the now growing number of methods of counting birds, and American Atlas leaders will be interested in the reports from other countries. Those papers that present the results of actual studies made in the Mediterranean region should be of considerable interest to community ecologists, as they report on a habitat unfamiliar to most North Americans. At an unheard of price by today's standards, the book is a bargain for everyone.—George A. Hall.

The Bee-eaters. By C. H. Fry. Buteo Books, Vermillion, South Dakota, 1984:304 pp., 8 color plates by the author, >100 drawings by John Busby. $47.50.—This is a well-

produced, pleasing, and informative volume on the 24 species of Meropidae. Bee-eaters are favorites of most who know them and it is surprising that it has taken so long for a modern book devoted solely to them to appear. (Dresser's monograph on the family was published a century ago.)

The preface sets forth the author's goals of summarizing existing knowledge and of describing "how races and species originate and to explain . . . their evolution." As the book is intended for the layman as well as the biologist, Dr. Fry avoids technical jargon whenever possible and attempts—quite successfully—to explain certain biological concepts in everyday terms. Another stated purpose of the book is to "publicize these admirable birds [so] that others may come to enjoy them too." It should do exactly that. The information presented is well documented and is supplemented by straightforward interpretation. I have been fortunate over the years to encounter a majority of the world's bee-eater species and this book has greatly enhanced my understanding of them.

An educational 12-page introduction presents the living bee-eater, discussing such things as the business of bee-eating, a little about tunnel excavation, other aspects of nidification, and migration. Nomenclature, classification, and enumeration of the forms recognized also are included here.

Chapter 2, devoted to the species accounts, occupies some 150 pages. Here the author sets down the "known salient biological characteristics" of each species, with the well-studied European Bee-eater (*Merops apiaster*) discussed most fully and in considerable detail (26 pages). (The little-known *Nyctyornis* species and the Celebes Bee-eater [*Meropogon forsteni*] merit only three pages each.)

The third chapter deals rather superficially, but interestingly, with species and subspecies origins. Based on climatic and vegetational changes in Africa and the degree of differentiation between northern and southern forms of the Carmine Bee-eater (*Merops nubicus*), Fry concludes that bee-eaters can evolve "practically to the species level" in fewer than 12,000 generations. The longer Chapter 7 also deals with evolutionary matters. It is concerned with the development of specific differences, considering various morphological characters plus ecological, social, and behavioral variation.

Other chapters are those covering food and foraging, bee-eaters in relation to apiculture, and social and reproductive life. There are nine appendices including a brief glossary, a listing of scientific names of mammals and birds other than bee-eaters mentioned in the text, dietary details of several species (from pellet examinations), and aberrant plumages. Following the appendices is a list of over 600 references cited in the text.

Dr. Fry's attractive and useful color plates (in Chapter 2) depict 42 species and subspecies. Facing each plate is a detailed map showing the distribution of all forms (including the 10 races not portrayed). The figures vary somewhat in quality, with those of *Nyctyornis* the least realistic, but all appear to be accurate. It is good to have at least a few juveniles represented, though I would have preferred more. Some species are shown nicely in small flight figures. Again, I wish all had been.

John Busby's drawings are exceptional and succeed wonderfully in capturing the very essence of bee-eater behavior in a wide variety of rarely-figured activities. We see birds hatching, flycatching, pursuing lizards, catching fish, excavating, shedding heat, water-bathing, rain-bathing, dust-bathing, basking, preening, wing-stretching, head-scratching, greeting, courting, copulating, threatening, fighting, bee-rubbing, regurgitating, "butterflying," roosting, and perching on animals. A series of drawings even illustrates novel types of reported but unconfirmed behavior including tool-using and one bee-eater carrying another.

Although most ornithologists truly enjoy the creatures they study, one would not always guess this to be true from what they write. Such is not the case with Hilary Fry. From the

preface of the book right through to the appendices, genuine affection for the subjects is evident. Bee-eaters truly are, to quote Dr. Fry, "altogether delightful birds." It is fitting that they have been dealt with in an altogether delightful book.—Dale A. Zimmerman.

Wood Warblers' World. By Hal H. Harrison. Technical assistance and range maps by Mada Harrison, foreword by Les Line. Simon and Schuster, New York, New York, 1984: 335 pp., 24 color plates, 218 black-and-white photographs, 53 range maps. $19.95.—This volume is the fulfillment of Harrison's 30-year dream to photograph as many of the wood warblers that nest in North America as possible, and to publish his work in book form. The author has succeeded, indeed, in photographing all but just a few species himself; the remainder have been supplied by a small group of his friends and fellow photographers. All 53 species of warblers regularly known to nest north of Mexico are pictured in this book; and in all but a single case (Bachman's Warbler [*Vermivora bachmanii*], where a photograph of a perched bird by John H. Dick is shown) either the bird at its nest or the nest and eggs have been included—usually both. There are also useful habitat shots illustrating typical breeding localities for each species. It is hard to imagine the difficulties of logistics and planning involved in depicting so many species of warblers in the few brief weeks available each breeding season, even over a period of 30 years. This is especially true when you consider that during much of this same time period the author was also attempting to photograph a few hundred additional species of birds for his two guides to bird nests for the Peterson series. Part of the answer lies in Harrison's almost uncanny ability to locate nests; from personal experience with him in the field, I can attest that few people today can equal his talent. The photographs, naturally, vary somewhat in quality, but all are at least very good and many are truly exceptional. A pair of Northern Parulas (*Parula americana*) at their nest, and two Bay-breasted Warblers (*Dendroica castanea*) feeding their young are especially fine examples of bird photography; a pair of Cerulean Warblers (*D. cerulea*) at the nest (in this case photographed by Betty Darling Cottrille) is superb.

In the text, which is written in a popular, nontechnical style, each species is given chapter status within which Harrison usually discusses migration, habitat, nesting sites, the nest and eggs, song, and behavior, along with an English translation of the scientific names. Emphasis throughout is on the breeding season, and little detail is provided on the winter habits or habitats of most species. The text is not simply a rehash of previously published accounts gleaned from the literature, but includes a great deal of original information based on the author's extensive field experience. This information is presented in a highly readable and entertaining style that is liberally laced with personal anecdotes. Budding bird photographers should pick up a wealth of helpful hints, as should field workers who need to know how and where to look for the nests of wood warblers. A glossary, a 12-page bibliography, and a well-prepared index add to the usefulness of the book. The introduction, however, is weak, trying as it does to pack too much information into too little space (half of the 19 pages allotted to this section are devoted to illustrations). The parulines are just too diverse a group to be summarized adequately so briefly.

Harrison's work supplements, rather than eclipses, earlier works on warblers such as Chapman's *Warblers of America,* Bent's *Life Histories,* or Griscom and Sprunt's *The Warblers of America,* and deserves space on the book shelf of any student of wood warblers.—Robert C. Leberman.

CRANES OF THE WORLD. By Paul A. Johnsgard. Indiana University Press, Bloomington, Indiana, 1983:258 pp., 23 color plates, 24 black-and-white plates, numerous maps, drawings, and tables. $37.50.—Cranes have been revered by man for centuries, but, in spite of this, most species are either endangered or declining. The author, who has studied the North American species and carefully researched the rest of the world's cranes, is well qualified to write this much-needed work. The Whooping Crane (*Grus americana*) has become a symbol of conservation here in the United States, and nearly all species of cranes hold a prominent place in the minds of people in their homelands. This concern has not prevented the continued decline in the numbers of most species of cranes over the last 50 years. Much of this is the result of a gross misunderstanding of the basic biology and habitat requirements of these birds.

In recent years a great deal of research has been conducted on cranes. In this book the author has put together the material needed to give us some insight into the biology of cranes. From this insight we have a better chance of helping to save members of this group of birds from extinction.

"Cranes of the World" is laid out in a very useful fashion with general comparative biology preceding the species accounts. The book contains a wealth of material on cranes in general as well as on each species. The color photographs are quite good, as are the sketches showing behavior and anatomy. The reference section seems complete and accurate. The tables are easy to read and are very helpful, providing quantities of data.

The author is to be commended for presenting the sections on aviculture and conservation as such prominent parts of the book. These topics are of prime importance today because of the endangered status of most species of cranes.

The only drawback of the book may be the low quality of paper. The cost of the book seems high, but considering the wealth of material it contains, the book is well worth the price. Certainly this is a must addition to all ornithological and avicultural libraries.—DONALD F. BRUNING.

VULTURE BIOLOGY AND MANAGEMENT. By Sanford R. Wilbur and Jerome A. Jackson (eds.). University of California Press, Berkeley, California. 1983:xxi + 550 pp., 82 line drawings, 58 half-tones, 61 tables. $35.00.—The idea for this comprehensive volume, which covers almost all aspects of vulture biology, was conceived at the First International Symposium on the Vultures, held in 1979, and much of the material contained in the book is based on talks given at that conference. The 38 contributors include authorities on vulture biology from around the world, thus the book unites much research that was previously scattered widely throughout the ornithological literature.

The first of 8 parts gives a brief, but unusually clear review of the paleontology and systematics of vultures. Part 2 surveys the worldwide status of vulture populations; regional reports are provided for southern Africa, Europe, France, Israel, Mongolia, the Indian subcontinent, the Western Hemisphere, and the Americas. Parts 3 and 4 contain chapters on various aspects of the biology of Old and New World vultures, respectively. Topics covered include growth and development, breeding behavior, adaptive radiation, migration, competition, and roosting behavior. Part 5 contains a number of useful papers on current research and management techniques for vultures. Part 6 reviews the problems vultures currently face as a result of environmental contaminants, and Part 7 describes the past and

present interactions between vultures and man. The final segment of the book is a 28-page bibliography of vultures that supplements the literature cited sections of each chapter.

"Vulture Biology and Management" provides a good introduction to the basics of vulture biology. It is also sufficiently detailed and up to date to be useful to those doing ongoing research in the area. The book is well-designed and handsomely printed and is thus not overpriced in terms of the current book market. Clearly, this comprehensive volume will prove invaluable for those interested in any aspect of vulture biology.—Nancy J. Flood.

Principles of Wildlife Management. By James A. Bailey. John Wiley and Sons, New York, New York, 1984:373 pp. $26.95.—Over the years there have been few textbooks covering the basic principles of wildlife management. Recently, however, there have been at least three such books of which this is the latest. There are 19 chapters presented within 5 parts: Wildlife Conservation, Wildlife Biology, Wildlife Ecology, Population Dynamics, and Wildlife Management. The book is well indexed, and 388 references are cited in a useful section at the end of the book. Illustrations are useful for the most part, and most chapters have specific examples or case histories which are well done. At the end of each chapter, the main "Principles" discussed are reviewed. The book is nicely bound, with a pleasant, glossy cover.

Chapters cover most of the standard material seen in such books; i.e., food, cover, reproduction, mortality, behavior, movements, and population dynamics. Several chapters go beyond what is normally found and provide interesting material on ecological succession, carrying capacity, data-base systems, and the art of wildlife management.

As I read Chapter 1, I could picture Dr. Bailey lecturing to undergraduate wildlife majors. Many good points were made, including the need for compromise in order to maintain the opportunity to play a role in decision making. There is also a discussion of the terms "wise use" and "harmony."

One problem I had with this text was the writing style. Certain terminology was used extensively, but it seemed very awkward to me. For example, on page 116 we find the term "species functions," on page 118 we find "cover resources," and on pages 206–207 we find "welfare factors" as well as "cover welfare factors." I found myself asking what these words meant. Other terms were used to the point where they became very distracting. For example, we find "welfare factor" 8 times on page 207.

Other minor problems included the definition of "trophy hunting" as the mere acquisition of something physical from the outdoors (p. 47), and the overall lack of a discussion of the growing problem of wildlife damage. There were few typographical errors, but one major error on the contents page stands out: the double listing of "Part III: Wildlife Ecology" and the omission of "Part II: Wildlife Biology."

These problems aside, I found the book useful and believe it will be used in many classrooms. Dr. Bailey is an imaginative wildlife biologist and professor who brings interesting and new philosophies into his classrooms and his writings. This book is no exception and should find considerable use by wildlifers and nonwildlifers alike.—David E. Samuel.

Birding with a Purpose. By Frances Hamerstrom, illus. by Jack Oar, with a Foreword by Joseph J. Hickey. Iowa State Univ. Press, Ames, Iowa, 1984:130 pp., 39 drawings, 16 black-and-white photographs, 1 map. $13.95.—Fran Hamerstrom writes as she thinks: in

short, crisp sentences, moving from thought to thought economically, pulling no punches. In an earlier collection of biographical sketches (Strictly for the Chickens, Iowa State Univ. Press, Ames, Iowa, 1980), Hamerstrom traced her and her husband Fred's exploits as "Prairie Chicken Biologists." In her latest volume, she uses her more than half-century of field experience both to teach and entertain readers. The lessons are short—chapters average about four pages—but informative and wry. Fran's "purpose" in birding is to study bird behavior, especially that of raptors, and her methods include banding and color marking. Her experiences provide a *précis* of what should and should not be attempted. Luckily for us, Fran is not afraid to describe her failures—and those of others—as well as her successes, and there is at least as much to learn from the former as from the latter. As Joe Hickey correctly notes in his Foreword, "This is not a stuffy book." After reading Fran's accounts of losing several Volkswagen minibuses through the ice while she searched for Snowy Owls (*Nyctea scandiaca*) on frozen Wisconsin lakes, I for one am not about to attempt to do the same! But then again, few but Fran would even conceive of such an adventure, especially in their spouse's vehicle.

The book opens with an informal but informative description of Hamerstrom's early attempts at color marking Black-capped Chickadees (*Parus atricapillus*), long before color marking became the standard operating procedure for behavioral studies. The formal results of these efforts are reported in "Dominance of winter flocks of chickadees" (Hamerstrom, Wilson Bull. 54:32–42, 1942), one of the first North American studies involving color-marked individuals. Similar essays describe the care and feeding of "gabboons"; the recent North American "evolution" of the bal-chatri, a device used in ancient India to catch accipiters; why "electric mice" do not work well in the field; why bananas are not to be fed to bait mice (*Mus musculus*); how burned-out light bulbs can be used to catch Bald Eagles (*Haliaeetus leucocephalus*); and how nylon stockings and road-killed woodchucks (*Marmota monax*) can be used to transmit messages to co-workers. Because it is written as a series of essays, the book can be savored in small bites as well as in one large meal. The work is well-edited and remarkably free of errors, save for the consistent and inexplicable misspelling of chickadee in the first chapter. It is spelled correctly thereafter. The sketches by Jack Oar complement the often humorous text in much the same way the illustrations in my dog-eared copy of Konrad Lorenz's "King Solomon's Ring" (Thomas Y. Crowell Co., 1952) complement that work.

For those who have not had the pleasure of dining and conversing with Fran at her home and research station in Plainfield, Wisconsin, the book will be an eye-opener. For those lucky souls who have made that trek, the book should rekindle numerous outrageous memories. Hamerstrom's book is "must" reading for graduate students about to begin their field work, as well as for anyone who views field research as a strictly sterile scientific undertaking.—K.L.B.

THE SCIENCE ALMANAC, 1985–86 Edition. By Bryan Bunch (ed.). Anchor Press/Doubleday, Garden City, New York, New York, 1984:xiv + 562 pp. $19.95 (hard cover), $12.95 (paper).—In the style and format of other almanacs, this new publication attempts to interpret the recent developments in science for the interested layman. The topics covered are Archaeology and Anthropology, Biology, Chemistry, Earth Science, Environment, Mathematics, Medicine, and Physics. Short essays outline developments in these fields, 1980–84, and sprinkled here and there are intriguing bits of "trivia." This appears to be a handy thing to have around.—G.A.H.

HANDBOOK OF THE BIRDS OF INDIA AND PAKISTAN. Vol. 4. Frogmouths to Pittas. Second Edition. By Salim Ali and S. Dillon Ripley. Oxford University Press, London, 1983:xvi + 267 pp., 11 color plates, numerous text figures and maps. $33.—A revision of a volume of this useful series originally published in 1970. Two new species are included and two others have been combined. There are three new color plates.—G.A.H.

PHYSIOLOGY AND BIOCHEMISTRY OF THE DOMESTIC FOWL. Vol. 5. By B. M. Freeman (ed.). Academic Press, London, England, 1984:436 pp., numerous black-and-white drawings and photographs. No price given.—This is the final volume of a work begun more than 10 years ago, of which Volume 4 was published in 1983 (see Review, Wilson Bull. 96:346, 1984). The 12 chapters cover topics dealing with metabolism, hormones, the cardiovascular system and blood groups, the lymphatic system, and reproduction.—G.A.H.

NORTH AMERICAN GAME BIRDS AND MAMMALS. By A. Starker Leopold, Ralph J. Gutiérrez, and Michael T. Bronson. Illus. by Gene M. Christman. Charles Scribner's Sons, New York, New York, 1984:ix + 198 pp., many line drawings and range maps. $12.95.—An unrevised paperback edition of a book originally published in 1981 and reviewed in Wilson Bull. 94: 607–608, 1982.—G.A.H.

Wilson Bull., 97(3), 1985, pp. 405–411

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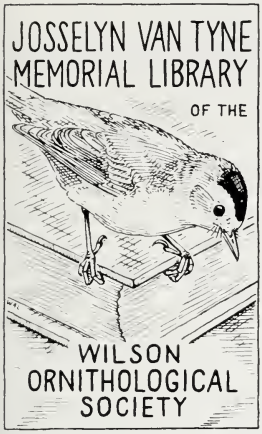

The following books have been added to the collection since the last book list was published in the September 1982 Wilson Bulletin (Wilson Bull. 94:393–429). The list includes books received both as gifts from members and on exchange, as well as those purchased with Library funds. It includes only those books that have been catalogued through December 1984. Any donations or contributions to the new book fund will be gratefully received and acknowledged. Members wishing to borrow these or any other items should write to the Library.

JANET HINSHAW, *Librarian, Wilson Ornithological Society, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109 USA. Telephone 313-764-0457.*

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ANNOUNCEMENTS

NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANTS

The North American Bluebird Society announces the third annual grants in aid for ornithological research directed toward cavity nesting species of North America with emphasis on the genus *Sialia*. Presently, three annual grants of single or multiple awards totaling $3000.00 are awarded and include:

Bluebird Research Grant.—Available to student, professional, or individual researchers for a suitable research project focused on any of the three species of bluebirds of the genus *Sialia*.

General Research Grant.—Available to student, professional, or individual researchers for a suitable research project focused on a North American cavity nesting species.

Student Research Grant.—Available to full-time college or university students for a suitable research project focused on a North American cavity nesting species.

Further guidelines and application materials are available upon request from Theodore W. Gutzke, Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746. Completed applications must be received by 31 January 1986; decisions will be announced by 15 March 1986.

RESEARCH GRANTS (CONT.)

The North American Bluebird Society is proud to announce the presentation of the second annual research grant awards. The 1985 recipients are as follows:

Bluebird Grant.—Patrick J. Mock (Topic: Reproductive Energetics in Relation to Brood Size in Western Bluebirds.)

General Grant.—Gregg M. Zuberbier (Topic: The Physiological Effects of *Protocalliphora* sp. Larvae on Nestling Growth.)

Student Grant.—Monica J. Schwalbach (Topic: Site Selection in the Eastern Bluebird.)

COST OF LIFE MEMBERSHIP IN WOS TO INCREASE

As of 1987, the cost of a Life Membership in the Wilson Ornithological Society will increase from the current bargain rate of $250 (payable in four annual installments of $62.50) to $400 (payable in four annual installments of $100). Those who are not already life members are urged to invest in this option. Life membership fees are added to the endowment fund and help support the Society indefinitely.

WOS CENTENNIAL FUND

In anticipation of the 100th anniversary of The Wilson Ornithological Society in 1988, the Executive Council has established a Centennial Fund. Members and friends of the society are asked to contribute to the fund, which will help support activities during our 100th year. Donations should be sent to the Treasurer, Robert D. Burns, Dept. Biology, Kenyon College, Gambier, Ohio 43022.

ALEXANDER WILSON GRAVE-SITE RESTORATION

Alexander Wilson, the Father of American Ornithology—and the man for whom the Wilson Ornithological Society is named—died in Philadelphia in 1813 while working on the ninth volume of "American Ornithology." Members and friends of the WOS are urged to contribute to the restoration of Wilson's grave site, which is located at Gloria Dei, "Old Swedes" church, in Philadelphia. The project will restore the immediate grave site and will increase the attractiveness of the surrounding cemetery to birds with suitable plantings. For more information, or to contribute, contact David M. Lauer, 1922 Bainbridge St., Philadelphia, Pennsylvania 19146 ([212] 985-0354). Make checks payable to the Scottish Historic and Research Society.

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Selected members of the *Tangara cayana* superspecies,
including (from top to bottom, males on right, females on left)
T. meyerdeschauenseei, sp. nov.; *T. vitriolina;* and *T. cayana.* Painting by John P. O'Neill.

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A NEW SPECIES OF TANAGER (EMBERIZIDAE: THRAUPINAE, *TANGARA*) FROM SOUTHERN PERU

THOMAS S. SCHULENBERG AND LAURENCE C. BINFORD

The thraupine genus *Tangara* is the largest genus of nine-primaried oscines and, in fact, of strictly New World birds. Thus we find it surprising that no new species of *Tangara* has been reported in over 70 years (see Nelson 1912), especially in view of the flood of avian novelties discovered during the last two decades of intensive ornithological exploration of Andean countries.

During field work in southern Peru for the Louisiana State University Museum of Zoology (LSUMZ) in the fall of 1980, we encountered an Andean population of *Tangara* that somewhat resembled *T. cayana* of the adjacent lowlands. Binford collected two of these birds, a male and a female. Subsequently we learned that Jean Dorst (1961) had collected two *Tangara* specimens in the same area in 1960. Study of these four specimens convinces us that this population represents an undescribed species that we propose to call

Tangara meyerdeschauenseei sp. nov.

GREEN-CAPPED TANAGER

HOLOTYPE.—Louisiana State University Museum of Zoology No. 98917; adult male, 2 km northeast of Sandia, ca. 2175 m, 14°17'S, 69°26'W, Department of Puno, Peru, 2 November 1980; collected by Laurence C. Binford, original number 1495.

DIAGNOSIS.—A large, relatively dull-colored, sexually dimorphic *Tangara*. Most similar to members of the *cayana* group, consisting of *T. cayana, T.* (*cayana*) *flava, T. cucullata,* and *T. vitriolina,* but differs in its greenish-straw, not orange-buff, chestnut, or rufous crown. The male is most similar to the male of *vitriolina* but may be distinguished by the greenish-straw, not rufous, crown; greenish-turquoise, not black, auriculars; greener (less blue) back and scapulars; and more uniform, grayish-buff underparts, lacking whitish on the lower

belly. Besides crown color, the male *meyerdeschauenseei* is best separated from the males of *cayana, flava,* and *cucullata* by the blue-green, not buff, straw, or greenish-straw, back and rump. The male further differs from the males of *cayana* and *flava* by the greenish-turquoise, not black, auriculars; by the grayish-buff, not warm buff or orange-buff, underparts; and by lacking the black throat and central belly stripe of *flava.* The male of *meyerdeschauenseei* lacks the extensive purple or blue opalescent colors of the underparts of the male *cucullata.* The female *meyerdeschauenseei* is very similar to females of *cayana, flava,* and nominate *cucullata,* differing primarily by the greenish-gold, not rufous, crown and by the greenish-gray, not dark gray, auriculars. The female is distinguished from females of *T. cucullata versicolor* and *T. vitriolina* by these same two characters, as well as by the generally cinnamon-buff, not deep ochraceous or buffy-white underparts, respectively.

DESCRIPTION OF HOLOTYPE.—The opalescence of the plumage causes some colors of the new species to vary under different viewing conditions. Blues and greens predominate when the light source is directly behind the observer; buff or straw colors predominate at other angles. In the following description, in cases in which the color of a region varies significantly depending upon the position of the light source, the region is first described as it appears when the light is behind the observer. This description is followed by the phrase "varying to . . . ," which describes the colors as they appear at other angles. Unless otherwise specified, this description is based on the colors as seen from a lateral view.

Lores and eye-ring dark gray. Auriculars greenish-turquoise, near Venice Green (capitalized color names from Ridgway [1912]), varying to dusky-gray with violet and gold overtones. Forehead (in frontal view) Light Blue Green, varying to grayish-buff. Crown greenish-straw, near Lumiere Green, varying to near Pale Orange-Yellow, contrasting at all times with color of back. Narrow superciliary, extending from lores to posterior border of eye-ring, blue-green, near Venice Green, varying to black. Center of back and rump Chrysopraise Green; sides of back, near scapulars, somewhat bluer than center; this entire region varying to coppery Cream Buff. Nape slightly bluer than back (including sides) when viewed with light directly behind observer, forming a faint bluish collar, not visible at other angles, at hind edge of crown. Scapulars near Tyrolite Green, varying to grayish-turquoise. Uppertail coverts blue-green, near Viridian Green. Tail, dorsal surface: central rectrices dark gray along shaft, elsewhere glossed with blue-green, brightest along outer edge of outer web; outermost pair of rectrices uniformly gray, very narrowly and faintly edged with blue-green on distal ⅓ of outer web; remaining rectrices gray on inner web and along shaft of outer web, rest of outer web blue-green, near Viridian Green, varying to coppery Cream Buff. Tail, ventral surface: outer rectrices pale gray, inner web and tip of outer web edged with blue-green, near Lumiere Green; remaining rectrices pale gray adjacent to shaft on inner web, elsewhere blue-green, near Deep Bluish Glaucous, varying to violet; the proportion of the inner web that is blue-green increases gradually from the outside in, to the central rectrices, which are almost entirely blue-green below. Wing, dorsal surface: upper wing coverts and remiges black to dark gray on inner web. Outermost primary entirely gray on outer web as well, rest of primaries narrowly edged with Light Oriental Green (varying to grayish-turquoise) on outer web, the extent of green edging present varying from basal ½ of primary (next-to-outermost primary) to almost complete length of outer web (inner primaries); outer web of secondaries and upper wing coverts broadly edged and tipped with Light Oriental Green (varying to grayish-turquoise). Chin pale grayish-turquoise. Throat and center of breast near Lavender Blue. Sides of breast and flanks grayish-buff, overlaid with green, near Lumiere Green. Center of belly Light Pinkish Cinnamon; lower belly nearer Warm Buff. Undertail coverts Warm Buff. Soft-part colors in life: iris brown; maxilla and tip of tomium of mandible black, rest of mandible pale gray; tarsi and toes lead gray.

MEASUREMENTS.—See Table 1 for measurements of the holotype and paratypes.

TABLE 1

RANGES AND MEANS OF MEASUREMENTS OF SELECTED *TANGARA* TANAGERS

	N	Wing chord (mm)	Tail (mm)	Tarsus (mm)	Culmen from base (mm)	N	Weight (g)
T. meyerdeschauenseei	1 ♂	79.1	59.8	18.3	14.3	1	26.5
	3 ♀♀	73.6–76.3 (75.0)	55.5–58.9 (56.9)	17.5–17.9 (17.7)	14.7–15.4 (15.0)[a]	1	25.4
T. vitriolina	5 ♂♂	72.9–77.0 (74.9)	52.1–56.9 (54.0)	16.2–17.9 (17.0)	14.4–14.7 (14.6)	4	20.2–24.6 (22.5)
	4 ♀♀	75.3–76.5 (75.6)	54.6–55.6 (55.0)	16.7–18.8 (17.5)	13.7–15.2 (14.6)	1	21.1
T. cayana	5 ♂♂	70.9–73.8 (72.5)	50.6–53.8 (52.0)	16.5–17.6 (17.1)	13.9–14.6 (14.1)	3	17.0–19.0 (18.0)
	4 ♀♀	68.6–72.7 (70.6)	47.6–52.3 (49.2)	16.7–18.0 (17.2)	13.8–14.3 (14.1)	3	19.0–22.5 (20.3)
T. (cayana) flava	10 ♂♂	70.0–77.0 (73.5)	47.6–57.2 (51.7)	15.7–18.3 (16.5)	13.3–14.8 (14.2)	—	—
	3 ♀♀	71.0–72.7 (71.7)	49.0–53.3 (51.3)	15.5–18.9 (17.4)	14.5–14.9 (14.7)	—	—
T. cucullata	10 ♂♂	72.9–78.5 (75.4)	50.1–54.6 (52.4)	17.7–20.0 (18.9)	14.7–16.7 (15.7)	—	—
	10 ♀♀	69.6–77.0 (73.3)	49.5–53.5 (51.2)	17.1–19.3 (18.3)	14.5–16.1 (15.3)	—	—

[a] N = 2.

DISTRIBUTION.—Known only from the Department of Puno, Peru, at Sandia (type locality); Asalay, ca. 13 km north of Sandia; and the west side of Abra de Maruncunca, ca. 14°14′S, 69°17′W, ca. 2000 m, ca. 20 km east of Sandia (sight records only). All localities are at the head of the Río Inambari, a tributary of the Río Madre de Dios (Fig. 1).

SPECIMENS EXAMINED.—In the following section, all unmodified locality names refer to departments, states, or provinces, and not to any cities that may bear similar names. *Tangara meyerdeschauenseei*: Sandia, Dept. Puno, Peru (type locality),1 ♂ (LSUMZ 98917; holotype), 2 ♀♀ (LSUMZ 98918; Muséum National D'Histoire Naturelle [=MNHN] C. G. 1962 No. 3263; paratypes); Asalay, ca. 13 km north of Sandia, Dept. Puno, Peru, 1 ♀ (MNHN C. G. 1962 No. 3262; paratype). *T. vitriolina* (all LSUMZ): Santander, Colombia, 2 ♀♀; Cauca, Colombia, 2 ♂♂, 1 ♀; Imbabura, Ecuador, 4 ♂♂, 1 ♀. *T. cayana* (all LSUMZ): Aragua, Venezuela, 1 ♂; Santander, Colombia, 1 ♂; San Martín, Peru, 2 ♂♂, 2 ♀♀; Madre de Dios, Peru, 1 ♂, 2 ♀♀. *T. (cayana) flava* (all LSUMZ): Pará, Brazil, 2 ♂♂; Goiás, Brazil, 5 ♂♂, 1 ♀; São Paulo, Brazil, 3 ♂♂, 2 ♀♀. *T. cucullata*: St. Vincent, Lesser Antilles, 4 ♂♂, 2 ♀♀ (collection of Albert Schwartz); and Grenada, Lesser Antilles, 1 ♂, 1 ♀ (LSUMZ), 5 ♂♂, 7 ♀♀ (Schwartz).

ETYMOLOGY.—We are pleased to name this new species after the late Rodolphe Meyer de Schauensee in recognition of his many contributions to Neotropical ornithology. In particular, his two books, *The species of birds of South America* (1966) and *A guide to the birds of South America* (1970), helped introduce a new generation of field ornithologists to the South American avifauna.

REMARKS

Description of female.—Dorst (1961) considered his two female specimens to be juvenile *Tangara cayana.* This is understandable, because they resemble dull-color adult female *T. cayana.* Nothing about the shape or texture of the feathers of these specimens, however, suggests immaturity and, because they are identical in plumage to the adult (based on skull ossification) female collected by Binford, they clearly also represent the new species.

The plumage of the female is similar in pattern to that of the male, but the green colors are more drab and the lavender of the chest is replaced with light green. Following is a description of the female: Lores and eye-ring dark gray. Auriculars dull green, near Peacock Green, mixed with light gray, varying to dusky-gray with gold overtones. Forehead (in frontal view) grayish-green, near Kildare Green. Crown yellow-olive, near Citron Green; hind edge of crown slightly greener, near Malachite Green; forehead and crown together varying to coppery gold, near Honey Yellow. Narrow superciliary, extending from lores to posterior border of eye-ring, slightly greener than crown, varying to dark gray. Back dull green, near Biscay Green, varying to near coppery Citrine Drab. Nape slightly bluer than back when viewed with light directly behind observer, forming a faint bluish-green collar, not visible at other angles, at hind edge of crown. Scapulars near Peacock Green, varying to dark gray. Rump paler than the back, near Malachite Green, varying to near Citrine Drab. Uppertail coverts blue-green, near French Green, varying to dark blue-green, near

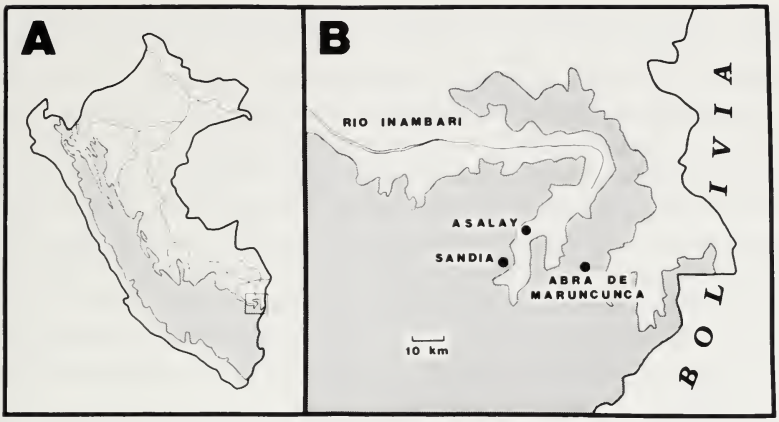

FIG. 1. A. The Andes Mountains of Peru (shaded within the 2000 m contour); the box at lower right encloses the headwaters of the Río Inambari. B. The headwaters of the Río Inambari, showing localities mentioned in the text.

Myrtle Green. Color pattern of rectrices similar to male, but green color of dorsal surface near French Green, varying to dark blue-green, near Myrtle Green. Underside of tail pale gray, faintly glossed with light green, varying to blue-green. Wing, dorsal surface: similar to male, but upper wing coverts edged with Peacock Green, varying to near Myrtle Green, and remiges (except for all-gray outer primary) edged with brighter green, near Calliste Green, varying to near Malachite Green. Chin pale whitish-gray. Throat and center of breast light green, near Light Cendre Green. Sides of breast and flanks buff, overlaid with green, near Light Cendre Green. Belly near Light Ochraceous-Buff. Undertail coverts Warm Buff. Soft-part colors of LSUMZ 98918 as in male. Bill of MNHN C. G. No. 3263 described as "gris plombé," with no mention of black (description probably incomplete).

Molt and breeding condition.—All four specimens were collected during the month of November. They show no excessive feather wear or molt other than the replacement of one rectrix (presumably lost accidentally) of the holotype. Gonad data are available for only two specimens, the male and female collected by Binford. The testes measured 9 × 6 mm each; the ovary measured 7 × 5 mm, with the largest ovum 1 mm. Although these data are not conclusive evidence of breeding, we suspect that *Tangara meyerdeschauenseei* might breed at this time of year because several forest-inhabiting *Tangara,* e.g., *xanthocephala* (Saffron-crowned Tanager), *vassorii* (Blue-and-black Tanager), and *viridicollis* (Silvery Tanager), were breeding in November 1980 at Abra de Maruncunca.

Systematic relationships.—To date, no systematist has formally proposed a phylogeny for *Tangara,* but several groups of species are generally regarded as natural. One such assemblage, the *cayana* group, consists of *T. cucullata* (Lesser Antillean Tanager), *T. vitriolina* (Scrub Tanager), and *T. cayana* (Burnished-buff Tanager; including the well-differentiated semispecies *flava,* the Stripe-bellied Tanager, which contains the taxa *huberi, flava, sincipitalis, chloroptera,* and *margaritae*). These taxa are characterized by relatively drab plumage, with buff or bluish-green colors predominating, a small degree of sexual dimorphism, and the presence of an orange-buff, chestnut, or rufous crown that contrasts somewhat with the color of the back. Members of the *cayana* group also share a greater affinity for semiopen habitats than do most of their congeners (Isler and Isler, in press).

The plumage, size (Table 1), and habitat (see below) of *Tangara meyerdeschauenseei* clearly mark it as belonging to the *cayana* group. Although the crown is not predominately orange-buff, chestnut, or rufous in color, buff tones do appear in certain lights. Furthermore, the crown of *meyerdeschauenseei* is somewhat set off from the color of the back, imparting a "capped" appearance, much as in other species of the *cayana* group.

The relationship of *Tangara meyerdeschauenseei* to other species within the *cayana* group is not clear. Both *meyerdeschauenseei* and *vitriolina* occur in the Andean highlands at similar elevations and in similar habitats. These two species are similar in size, averaging larger in wing and tail length and in weight (Table 1) than *cayana,* geographically the closest member of the *cayana* group to both species. That both species are larger than *cayana* is not necessarily indicative of close relationship between them because montane Andean taxa tend to be larger than related taxa of lower elevations (Traylor 1950). The evidence from plumage pattern is also equivocal. Although the male plumages of *meyerdeschauenseei* and *vitriolina* are similar, the female of *meyerdeschauenseei* is more like the female of *cayana.* Furthermore, the male of *meyerdeschauenseei* (as well as of *vitriolina*) basically resembles the female of *cayana,* with the female *cayana*'s dull green colors replaced by shiny opalescent green (*meyerdeschauenseei*) or blue (*vitriolina*). We conclude that *meyerdeschauenseei* shares many similarities with, and appears to be closely related to, both *vitriolina* and *cayana.*

Regardless of whether *Tangara meyerdeschauenseei* and *vitriolina* are more closely related to each other than to other members of the *cayana* group, we believe that recognition of *meyerdeschauenseei* as a distinct species is warranted. We base this conclusion on its unique plumages in both sexes, which render it as distinct from *vitriolina* as the latter is from

cayana, and on the similarity of the female to *cayana* rather than to *vitriolina.*

Habitat and distribution.—We made most of our limited observations of the new species near Sandia, in the deep valley of the upper Río Inambari. The narrow floor and steep sides of the valley are extensively farmed. Where not cleared or too rocky, the slopes are covered with dense evergreen shrubs 2–3 m tall. Whether this scrub habitat is a consequence of prolonged human disturbance or of the rain shadow effect of the high valley walls, we cannot be certain, although the latter seems more likely. Here we found *Tangara meyerdeschauenseei,* typically in pairs or singly, to be fairly common in fruiting trees in small *chacras* (garden plots) or in semiarid scrub along the small river flowing past the village. The stomachs of the two birds collected by Binford contained fruit pulp and seeds as large as 8 × 4 mm.

Disturbance of the natural vegetation is more recent and complete in the vicinity of Abra de Maruncunca. The pass (*abra*) is crossed by the road running from Sandia east to San Juan del Oro. North of the road the pass remains covered with tall cloud forest, which, at the time of our visit, was being subjected to selective logging by the local people. Extensive areas south of the road at the pass, and along the road east and west of the pass, however, are almost completely clear-cut; the remaining forest is restricted to gullies and very steep slopes. On 5 November 1980, Schulenberg found *Tangara meyerdeschauenseei* to be fairly common along the edge of these cleared areas west of the pass.

The avifauna currently associated with *Tangara meyerdeschauenseei* in the Sandia area contains at least two elements. Some species, in the Peruvian portions of their ranges, are typical of montane scrub zones, e.g., *Synallaxis azarae* (Azara's Spinetail), *Myiotheretes striaticollis* (Streak-throated Bush-Tyrant), *Turdus chiguanco* (Chiguanco Thrush), *Thraupis bonariensis* (Blue-and-yellow Tanager), and *Saltator aurantiirostris* (Golden-billed Saltator). Other species are inhabitants primarily of lowland open areas, e.g., *Tyrannus melancholicus* (Tropical Kingbird) and *Thraupis episcopus* (Blue-gray Tanager), having invaded the Sandia valley as it has been opened for agriculture. We believe that *Tangara meyerdeschauenseei* is a true montane form and not simply another recent invader from lower elevations. *Tangara cayana* has been collected (LSUMZ) at the Pampas de Heath (ca. 13°00′S, 69°00′W, Dept. Madre de Dios, Peru, a large area of savannah at 160 m only 150 km NNE of Sandia) (see Graham et al. 1980). We presume that if *meyerdeschauenseei* were truly a lowland form, it too would have been found on the Pampas de Heath. In this part of Peru, we know of no other extensive areas of open or semiopen habitats such as those frequented by this species.

The elevational distribution and habitat of *Tangara meyerdeschauenseei* are probably similar to those of *vitriolina,* which is found in semiarid intermontane valleys of western Colombia and Ecuador between 1100 and 2400 m (occasionally as low as 500 m). We suspect that *meyerdeschauenseei* eventually will be found in other such valleys in southern Peru and northern Bolivia. Despite the small extent of its known range, we doubt that this species is in any immediate danger of extinction. Because it appears to inhabit semiopen rather than forested regions, continued clearing of forests may actually favor this species.

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GENETIC EVIDENCE FOR RELATIONSHIPS AMONG THE RED-EYED, YELLOW-GREEN, AND CHIVI VIREOS

Ned K. Johnson and Robert M. Zink

One of the most enduring puzzles in the systematics of New World birds concerns the relationships and taxonomic status of forms in the Red-eyed (*Vireo olivaceus*)-Yellow-green (*V. flavoviridis*)-Chivi Vireo (*V. chivi*) complex. In recent decades, the latter two taxa have been treated either as distinct species (A.O.U. 1957, Hamilton 1962) or as races of the Red-eyed Vireo (Hamilton 1958, Barlow 1980, A.O.U. 1983). Arguments for specific status of the Yellow-green Vireo have stated that this form has a wing formula (Eisenmann 1962) and advertising song (Borror 1972) distinctive from those of the Red-eyed Vireo and Chivi Vireo, and have emphasized the lack of definitely intermediate specimens between *flavoviridis* and either other form. No hybrids have been recorded despite the fact that the known breeding range of the Yellow-green Vireo approaches that of the Red-eyed Vireo in southern Texas (Eisenmann et al. 1968, A.O.U. 1983) and is contiguous with that of the Chivi Vireo near the border of Panama and Colombia (Eisenmann 1962). Reasons for subspecific treatment for both *flavoviridis* and *chivi* have stressed that (1) *olivaceus, flavoviridis,* and *chivi* are all allopatric during the breeding period; (2) plumage differences among them are either minor (*olivaceus* and *chivi* vs *flavoviridis*) or subtle (*olivaceus* vs *chivi*); and (3) their songs are generally similar (Slud 1964, Robbins et al. 1966, Barlow 1981). All forms of *olivaceus* and *flavoviridis* have red irides as adults and brown irides as immatures. In contrast, insofar as we have been able to determine from the literature and from specimen tags with eye color information, the forms of *chivi* have brown irides at all ages. Eye color of adults is thus the only obvious difference between *chivi* and *olivaceus*.

Oddly, the breeding ranges of the two most similar forms, *olivaceus* in North America and *chivi* in South America, are separated by all of Middle America, which is the nesting distribution of the more distinctive form, *flavoviridis* (Barlow 1980). Such a geographic-phenotypic pattern is reminiscent of the situation seen even more strikingly in a number of avian taxa in the Andes (Remsen 1984). In view of this peculiar geographic layout, systematists have been reluctant to take an intermediate stance in their classification of these vireos, namely, to combine two of the taxa as subspecies of one species while giving species status to the remaining

taxon. Nonetheless, the evidence on genetic differentiation presented here supports exactly such a position. We propose that the two geographically disjunct taxa, *olivaceus* and *chivi,* are conspecific but that the form that occurs between them, *flavoviridis,* deserves species rank. Although we studied only the subspecies *diversus* from Paraguay, all forms of the Chivi Vireo are considered here to be subspecies of the Red-eyed Vireo. Admittedly, eventual genetic study of the other geographic differentiates of *chivi* could provide results that might drastically alter this position.

The genic data, considered together with the current breeding distributions of the taxa, also enable a more objective discussion of phyletic history than heretofore has been possible. Unfortunately, we lack genetic information from several other forms of the genus, including the Black-whiskered Vireo (*V. altiloquus*), Yucatán Vireo (*V. magister*), and the Golden Vireo (*V. hypochryseus*). Although some or all of these species are probably closely related to the *V. olivaceus-flavoviridis-chivi* complex (Hamilton 1962, Barlow 1980), in the absence of data on genetic distances we do not consider them further in this paper.

MATERIALS AND METHODS

Our analysis is based on 17 specimens of the Red-eyed Vireo (*V. o. olivaceus*), one specimen of the Yellow-green Vireo (*V. f. flavoviridis*), 14 specimens of the "Chivi" Vireo (*V. o. diversus*), and one specimen of the Rufous-browed Peppershrike (*Cyclarhis gujanensis ochrocephala*). The latter form was used as an outgroup taxon.

Samples of heart, liver, kidney, and pectoral muscle were removed from specimens 1–4 h after collection in the field, preserved in liquid nitrogen, then stored in Berkeley, California, at −76°C (Johnson et al. 1984). Tissue extracts were prepared for electrophoresis according to methods described by Selander et al. (1971). Gel and buffer combinations used were essentially those outlined by Yang and Patton (1981). Thirty-eight presumptive genetic loci were scored. Although some loci were scored on more than one gel type, our basic approach was "one pass" (Aquadro and Avise 1982). Precise electrophoretic conditions are available from the authors. The most common allele at a locus was designated M; alleles with more anodal or cathodal migrations were coded as F or S, respectively. Further refinements in migratory position were coded with plus and minus signs.

The distribution of observed and expected numbers of heterozygotes (Table 1), over all loci in a sample, was tested for departure from Hardy-Weinberg expectation (Hartl 1981) with a χ^2 test (Barrowclough 1980). Individual heterozygosity was calculated by dividing the number of loci at which an individual was heterozygous by the total number of loci scored (38 for all birds). Two measures of average individual heterozygosity per population sample ($H_{obs.}$ and $H_{exp.}$) were calculated as described in Johnson and Zink (1983:873). Individual genotypes were converted to allelic frequencies (Table 2) for each sample. Genetic distances between samples (Table 3) were computed using the methods of Nei (1978) and Rogers (1972). Branching diagrams depicting patterns of genic similarity among samples (Fig. 1) were constructed using the methods of Sneath and Sokal (1973; UPGMA and WPGMA phenograms), Farris (1972; distance Wagner tree, optimized according to Swofford [1981]), and Fitch and Margoliash (1967; "F-M" trees).

TABLE 1
GENETIC VARIABILITY MEASURES FOR FOUR TAXA OF VIREONIDAE

Taxon	N	Sample area[a]	H_{obs} ± SE	H_{exp} ± SE	Percent polymorphic loci[b]	Average number of alleles[c]
V. o. olivaceus	17	Minnesota (15) Oklahoma (2)	0.059 ± 0.014	0.054 ± 0.017	39.47	1.53
V. o. diversus	14	SE Paraguay	0.060 ± 0.016	0.065 ± 0.025	26.32	1.47
V. f. flavoviridis	1	Costa Rica	0.0	0.0	0.0	1.00
C. g. ochrocephala	1	SE Paraguay	0.053	0.026	5.26	1.03
Total	33					
Mean[d]			0.057	0.036	17.76	1.26

[a] Breeding specimens only. Exact localities can be obtained from the authors.
[b] Frequency of most common allele ≤0.99.
[c] Per locus.
[d] Unweighted by sample size.

RESULTS

Variation at loci and heterozygosity.—Of the 38 loci scored, 19 (50%) showed at least a single heterozygote. At five other loci, the species were fixed at alternative alleles. Therefore, 24 (63.2%) of the total loci were variable among the taxa examined. Allelic frequencies at the polymorphic loci are listed by taxon in Table 2. The 14 monomorphic loci, within and between taxa, were: LDH-1, AB-1, AB-2, AB-3, LAP, SOD-1, EAP, GOT-1, GOT-2, MDH-1, MDH-2, GLUD (=GDH), ADH, and EST-1. Acronyms for enzymes follow Harris and Hopkinson (1976).

The observed and expected heterozygosities, the percentage of polymorphic loci and the mean number of alleles per locus for the four taxa of vireonids treated are given in Table 1. The fact that we examined only a single individual each of *V. f. flavoviridis* and *C. g. ochrocephala* presents no problem in the estimation of either mean levels of heterozygosity or genetic distance. According to theoretical (Nei 1978) and empirical (Gorman and Renzi 1979) rationales, good estimates of these parameters can be obtained from single specimens, given that a relatively large number of loci is analyzed and that heterozygosity is relatively low.

Values for observed heterozygosity for *V. o. olivaceus* and *V. o. diversus* were 0.059 and 0.060, respectively (Table 1). These values are somewhat higher than 0.048, the figure reported by Avise et al. (1982:97) for a large sample of *V. olivaceus* (presumably *V. o. olivaceus*), and 0.053, the average value reported for birds in general by Barrowclough (1983). In average

TABLE 2

ALLELIC FREQUENCIES FOR POLYMORPHIC LOCI IN THREE TAXA OF *VIREO* AND IN *CYCLARHIS GUJANENSIS OCHROCEPHALA*

Locus	*V. o. olivaceus* (N = 17)	*V. o. diversus* (N = 14)	*V. f. flavoviridis* (N = 1)	*C. g. ochrocephala* (N = 1)
GPI	A = 0.03, B = 0.97	A = 0.04, B = 0.96	B = 1.00	B = 1.00
NP	B = 0.79, C = 0.21	A = 0.18, B = 0.46, C = 0.29, D = 0.04, F = 0.04	B = 1.00	E = 1.00
CK	A = 1.00	A = 1.00	A = 1.00	B = 1.00
LGG	B = 0.77, C = 0.24	A = 0.25, B = 0.68, C = 0.07	B = 1.00	B = 1.00
LA-1	C = 0.94, D = 0.06	B = 0.04, C = 0.96	C = 1.00	A = 0.50, C = 0.50
LA-2	B = 0.94, C = 0.03, D = 0.03	A = 0.11, B = 0.86, D = 0.04	B = 1.00	B = 1.00
GDA	A = 0.94, C = 0.06	A = 1.00	B = 1.00	A = 1.00
EST-4	B = 0.03, C = 0.97	C = 0.93, D = 0.07	B = 1.00	A = 1.00
αGPD	B = 1.00	B = 1.00	C = 1.00	A = 1.00
ALD	A = 1.00	A = 1.00	A = 1.00	B = 1.00
6-PGD	A = 0.09, B = 0.88, C = 0.03	B = 1.00	B = 1.00	B = 1.00
ADA	C = 0.97, D = 0.03	C = 1.00	C = 1.00	A = 0.50, B = 0.50
MPI	B = 0.03, D = 0.97	B = 0.04, C = 0.04, D = 0.93	D = 1.00	A = 1.00
SDH	A = 1.00	A = 0.96, B = 0.04	A = 1.00	C = 1.00
GPT	A = 1.00	A = 1.00	A = 1.00	B = 1.00
ME	A = 0.94, B = 0.03, D = 0.03	A = 1.00	A = 1.00	C = 1.00
GSR	B = 1.00	B = 1.00	A = 1.00	A = 1.00
PGM-1	A = 0.79, B = 0.21	A = 0.96, B = 0.04	A = 1.00	B = 1.00
PGM-2	C = 0.06, E = 0.94	A = 0.04, B = 0.04, C = 0.61, E = 0.32	D = 1.00	D = 1.00
ICD-1	A = 0.03, B = 0.15, C = 0.03, D = 0.79	D = 1.00	D = 1.00	D = 1.00
ICD-2	A = 0.97, B = 0.03	A = 1.00	A = 1.00	A = 1.00
ACON	B = 1.00	B = 1.00	B = 1.00	A = 1.00
LDH-h	A = 1.00	A = 1.00	A = 1.00	B = 1.00
CK-h	A = 1.00	A = 1.00	B = 1.00	C = 1.00

TABLE 3
MATRIX OF GENETIC DISTANCES BETWEEN FOUR TAXA OF VIREONIDAE[a]

	V. o. olivaceus	*V. o. diversus*	*V. f. flavoviridis*	*C. g. ochrocephala*
V. o. olivaceus	—	0.014	0.177	0.533
V. o. diversus	0.053	—	0.176	0.528
V. f. flavoviridis	0.188	0.182	—	0.495
C. g. ochrocephala	0.427	0.419	0.391	—

[a] Nei's (1978) *D*-values are above the diagonal and Rogers' (1972) *D*-values are below the diagonal.

number of alleles per locus, *V. o. olivaceus* and *V. o. diversus* were also very similar (1.53 vs 1.47, respectively). No genetic variation was detected in the single individual of *V. f. flavoviridis.* The specimen of Rufous-browed Peppershrike had only two heterozygous loci (LA-1 and ADA). The observed number of heterozygotes in both samples of the Red-eyed Vireo (sensu lato) did not differ from Hardy-Weinberg expectation: *V. o. olivaceus,* $\chi^2_9 = 5.1$; *V. o. diversus,* $\chi^2_{10} = 6.3$.

When the four taxa were compared at specific loci, several major differences were seen (Table 2). For example, *V. f. flavoviridis* is apparently fixed at an allele which is different from the predominant one shared by *V. o. olivaceus* and *V. o. diversus,* at GDA, EST-4, αGPD, GSR, PGM-2 and CK-h. *C. g. ochrocephala* is apparently fixed at a unique allele at 13 (54.2%) of the 24 variable loci: NP, CK, EST-4, αGPD, ALD, ADA, MPI, SDH, GPT, ME, ACON, LDH-h, and CK-h, indicating large differences between it and the forms of *Vireo.*

Some differences in relative variability at particular loci were also evident. At both 6-PGD and ME, *V. o. olivaceus* had three alleles whereas *V. o. diversus* was fixed. At PGM-2, *V. o. diversus* showed four alleles whereas *V. o. olivaceus* had two. Furthermore, at that locus, the predominant allele was different in the two taxa. Otherwise, these two taxa, considered to be conspecific in this paper, are very similar in allelic frequency distributions.

Genetic distances.—Rogers' (1972) and Nei's (1978) values for genetic distances among the four taxa treated are given in Table 3. *V. o. olivaceus* and *V. o. diversus* are genetically very similar (Nei's $D = 0.014$). On the other hand, both *V. o. olivaceus* and *V. o. diversus* are quite different from *V. f. flavoviridis,* and at a nearly identical level ($D = 0.177$ and 0.176, respectively). The outgroup, *C. g. ochrocephala,* differed substantially ($D = 0.519$) from the three taxa of *Vireo.*

Phenograms and phylogenetic trees.—Despite the continuing debate over the suitability of different methods of branching (see Farris 1981

contra Felsenstein 1984) for describing phylogenies, we find that they reveal structure in the genetic data and are helpful in "visualizing" genetic distances. Also, because of the differing assumptions of each technique (e.g., relative homogeneity of rates of allozymic change), different kinds of information are revealed. In the present study, great congruence of pattern was achieved. The UPGMA and WPGMA clustering procedures (Sneath and Sokal 1973), for example, yielded virtually identical results; therefore, only the former is illustrated (Fig. 1A). All diagrams clearly show the close alliance of *V. olivaceus* and *V. "chivi,"* the more distant attachment of *V. flavoviridis* as a sister group to the first pair of forms, and the great separation of *C. gujanensis* from the clade comprised of the three forms of *Vireo*. We feel confident, therefore, that the consistent pattern of branching achieved in these analyses was not a simple result of the methodology employed (Presch 1979). That is, the branching pattern was independent of assumptions regarding the nature of the data.

DISCUSSION AND CONCLUSIONS

Age of the Taxa

Several researchers (e.g., Nei 1975, Sarich 1977, Yang and Patton 1981, Gutierrez et al. 1983) have attempted to determine the absolute timing of cladogenetic events by various calibrations applied to Nei's *D* values among existing species. Gutierrez et al. (1983), for example, used the mid-Miocene date of a fossil quail, *Cyrtonyx cooki* (Wetmore 1934), in conjunction with average genetic distances between modern *Cyrtonyx montezumae* and its Odontophorine sister taxa, to derive a calibration value of $t = 26.3 \times 10^6 D$, where t is the time since divergence and D is Nei's (1978) genetic distance. Such calibrations are dependent on the existence of a molecular clock (Wilson et al. 1977, Thorpe 1982), that is, a process by which nucleotide substitutions and, therefore, allelic differences among populations and species accumulate stochastically through mutation and drift in a uniform, time-dependent fashion. The recent finding of Barrowclough et al. (1985) that patterns of genetic divergence in diverse taxa of birds agree with the predictions of a neutral, mutation-drift process (Kimura 1979, 1982) lends credence both to the existence of a clock and to these dating attempts.

Nonetheless, several problems attend the use of such calibrations: (1) the relative imprecision of the dating of most fossils, including that of the quail mentioned above; (2) the fact that large standard errors are usually associated with estimates of genetic distance; and (3) the typical lack of independent means, beyond general stratigraphic date or degree of morphologic change, by which to judge the validity of divergence times

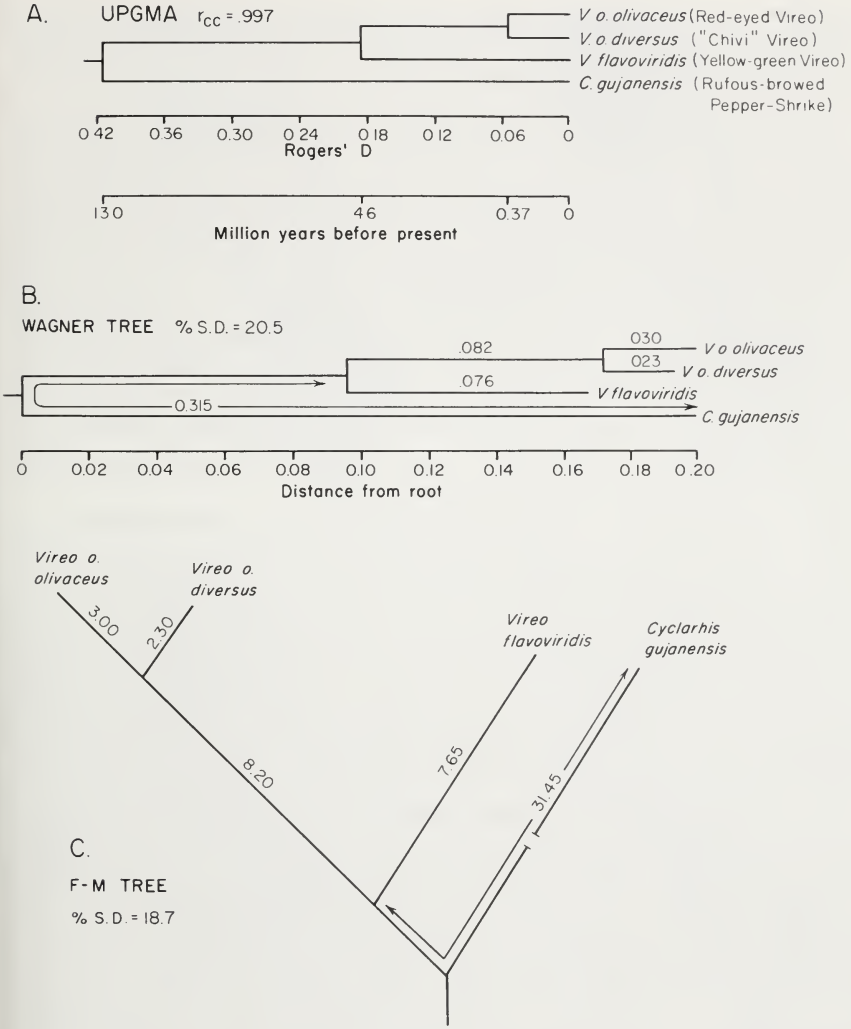

FIG. 1. (A) Phenogram based on Rogers' *D*-values (Table 3) and derived by the UPGMA method. The high cophenetic correlation coefficient ($r_{cc} = 0.977$) indicates very close agreement between the distances shown in the phenogram and the original distance matrix. See text for the derivation and interpretation of the time scale. (B) Distance Wagner Tree rooted at the outgroup, *Cyclarhis gujanensis*. The *F*-value (Farris 1972) is 0.002 and the cophenetic correlation is 1.00. This analysis produced no negative branches. (C) Branching diagram derived by the method of Fitch and Margoliash (1967). Branch lengths are in units of Rogers' *D* (×100). The tree is "rooted" (see Farris 1972) at *Cyclarhis gujanensis*. Of 6 F-M Trees examined, the one illustrated best summarized the original matrix based on the lack of negative branches and lowest percentage standard deviation.

calculated in this manner. Despite these caveats, gross approximations of cladogenetic dates are useful because they offer a hypothetical framework within which *possible* phyletic history can be addressed. Without such estimates, one is left with the alternative of blind speculation.

According to the calibration of Gutierrez et al. (1983), the Nei's genetic distance of 0.495 between *V. f. flavoviridis* and *C. g. ochrocephala* indicates that the ancestors of these two taxa split approximately 13 million years before the present (MYBP), or in the late Miocene (Fig. 1A). Subsequent separation of the lineage leading to *V. olivaceus*-"*chivi*" from that leading to *flavoviridis,* which differ by a Nei's *D* of 0.176, occurred at approximately 4.6 MYBP, in the late Pliocene. Finally, the small Nei's *D* (0.014) recorded between *V. o. olivaceus* and *V. o. diversus* (="*chivi*") suggests that these taxa diverged comparatively recently, on the order of 370,000 years ago, during the Pleistocene. The substantial, formally recognized geographic variation of *V.* "*chivi*" in South America (10 subspecies, Blake 1968) is in keeping with such a date.

Avise et al. (1982) reported that congeneric vireos are separated by genetic distances that average considerably higher than those between congeneric species in other passerine families. On these grounds they suggested that speciation events in *Vireo* may have been older compared with those of other groups. Our finding of a relatively large genetic distance between *flavoviridis* and both *olivaceus* and *chivi* provides corroboration of their result. We are currently examining the issue of increased genetic distances among vireos through the electrophoretic analysis of additional forms, including several species not studied by Avise et al. (1982).

The substantial genetic distance between *Cyclarhis* and the members of *Vireo* is perhaps not surprising in view of the fact that the pepper-shrikes have often been considered on other grounds to represent either a distinct subfamily or a distinct family (Cyclarhidae) related to the Vireonidae. Based on evidence from DNA-DNA hybridization, however, Sibley and Ahlquist (1982) concluded that *Vireo* and *Cyclarhis* were similar enough to be placed in the same subfamily. This apparent disagreement between the data from electrophoresis and those from DNA-DNA hybridization cannot be resolved at present. But it is clear that any explanation proposed for the difference must take into account the unusually large genetic distances now known among vireos and their close relatives.

Historical Biogeography of the Taxa

The unambiguous genetic results permit evaluation of possible historical biogeographic events that led to the observed geographic pattern. From many conceivable speculative scenarios, we depict four diagrammatically (Fig. 2). In these diagrams, the breeding range of the ancestral

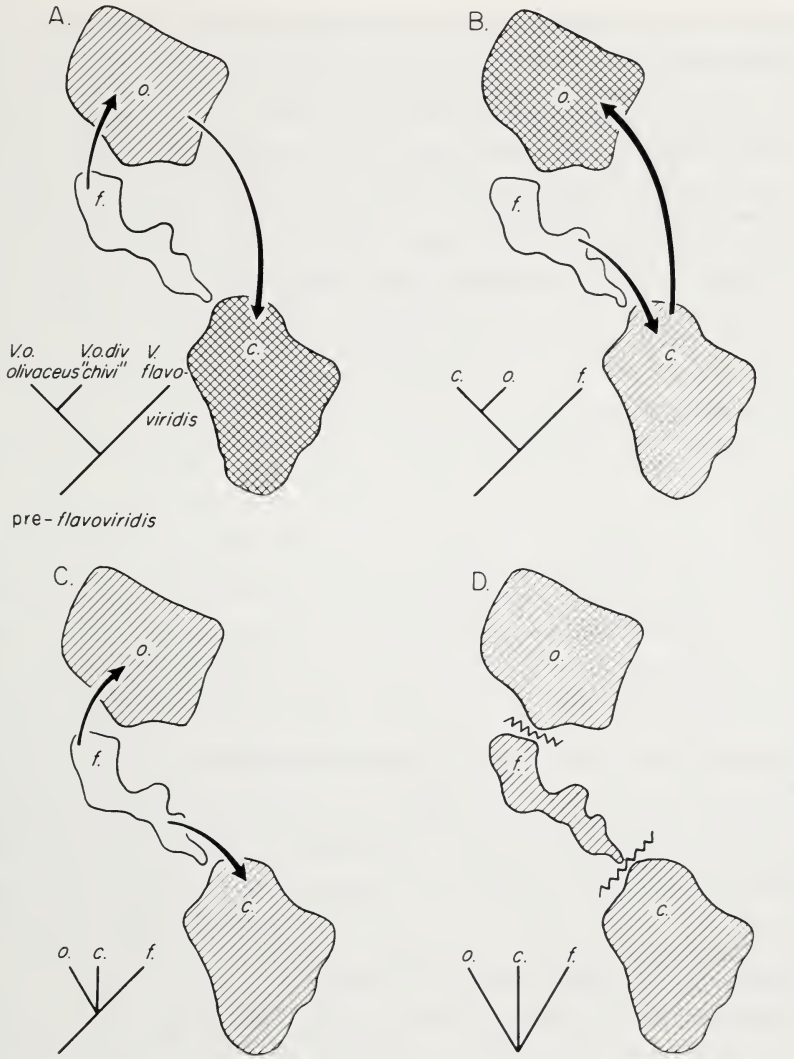

FIG. 2. Schematic representations of four hypothetical scenarios of the biogeographic history of *Vireo olivaceus, V. flavoviridis,* and *V.* "*chivi*" in North, Middle, and South America, respectively. See text for additional explanation.

taxon is unpatterned, that of the first derivative taxon is single-hatched, and that of the most recently derived taxon is crosshatched. The first three scenarios (A–C) are dispersal models. These assume that the ancestral taxon occupied part or all of one of the three current ranges and

dispersed to and differentiated in the remaining two distributions after simple colonization followed by range expansion. The fourth scenario (D), a vicariance model, assumes that much or all of the present combined range of the three taxa was occupied by a common ancestor that occurred through North, Middle, and South America. Subsequent fragmentation of all or part of this ancestral distribution provided for the isolation necessary for the differentiation of *olivaceus, flavoviridis,* and *chivi.*

Many other more complex models, which involve either colonization or vicariance processes, admittedly are possible. Models that conceive of the origin of *V. flavoviridis* in South America, with subsequent budding of *V. olivaceus* and *V. chivi,* are also plausible. None of these more intricate models is considered here in detail because in our view one of the simple models presented in Fig. 2 adequately explains the observed data.

Scenario A.—This phylogenetic hypothesis proposes that pre-*flavoviridis* or *flavoviridis* was ancestral and originated in Middle America. It gave rise to *olivaceus,* which, in turn, spawned *chivi* through leapfrog fall migration over the centrally located taxon. Presumably, *chivi* arose through colonization of South America by wintering individuals of *olivaceus* that failed to return to their breeding grounds. This scenario (1) is in agreement with the morphologic and genetic distinctiveness of *flavoviridis* compared with the similarity of *olivaceus* and *chivi*; (2) implicates the present migratory patterns as possible clues to phyletic events; (3) permits the ancestral taxon, *flavoviridis,* to occupy an intermediate "refuge-position" during late Pliocene-Pleistocene climatic refrigeration; (4) allows colonists from pre-*flavoviridis* to establish *olivaceus* as habitats became available to the north after glaciation; and (5) is in keeping with a Middle American center of diversification for the Vireonidae, as suggested by Hamilton (1962, but see Cracraft 1973:518). Furthermore, this hypothesis does not require us to invoke rapid evolutionary rates in *flavoviridis,* versus more moderate rates of change in *olivaceus* and *chivi,* to account for the greater phenetic-genetic differences of the former taxon.

Vireo flavoviridis is also migratory, with populations moving between the breeding grounds in Mexico and Middle America and the wintering regions in Amazonia. Morton (1977) has suggested that both the present scheduling of annual movement and the ultimate selective reason for the evolution of migration in this vireo are related to the seasonal scarcity of fruit in the nesting region. Whatever the reason, the fact of migration in this species in no way reduces the likelihood of Scenario A; a *nesting* population of either pre-*V. flavoviridis* or of *V. flavoviridis* presumably would have provided the stock that eventually budded off the ancestors of *V. olivaceus* to the north.

Scenario B.—This scenario resembles the one depicted in Fig. 2A in

that it suggests a stepwise origin of the two derivative taxa, *olivaceus* and *chivi,* from ancestral *flavoviridis.* In this scenario, however, colonists leading to *chivi* budded off first; these then gave rise to *olivaceus* by a northward leapfrog movement over *flavoviridis.* The fact that southern populations of *chivi* are presently migratory and move north in the late austral summer perhaps provided in the past the possibility for migratory overshoot by groups that became established north of *flavoviridis* and then evolved into *olivaceus.* Several tropical or subtropical species with migratory populations in the Southern Hemisphere (e.g., Fork-tailed Flycatcher [*Muscivora tyrannus*] and Tropical Kingbird [*Tyrannus melancholicus*]) currently are vagrant to North America (National Geographic Society 1983) and provide examples of such migratory overshoot.

Scenario C.—This scenario assumes that both *olivaceus* and *chivi* arose independently, and in essentially the same span of time, from ancestral *flavoviridis.* The improbability that separate groups of colonists from *flavoviridis,* moving northward and southward, respectively, would by chance be nearly identical genetically, however, renders this suggestion unlikely.

Scenario D.—This scheme derives modern *flavoviridis, olivaceus,* and *chivi* from an extensive and continuous range that underwent fragmentation. In this model, migration evolved in the various isolated taxa after their initial split. This scenario also requires more rapid evolution in the component that led to *flavoviridis,* than in the sections that evolved into *olivaceus* and *chivi,* to account for the greater genetic and phenetic differences of the former taxon. The degree to which the invocation of rapid evolution presents a problem is debatable. On the one hand, it is well-documented that differences in morphology and coloration in birds can evolve quickly (Johnston and Selander 1964, 1971). On the other hand, rapid genetic change seems less likely, especially in view of the findings of Barrowclough et al. (1985).

Although any of these schemes is plausible, we prefer Scenario A. It is simple because it does not require the added assumption of differing evolutionary rates of genes among the three taxa, and, most importantly, is realistic. Modern populations of *olivaceus* migrate annually to Amazonia to spend the winter. These wintering hordes of *olivaceus* in South America could have provided abundant opportunity in the past for the establishment of breeding colonies that evolved into *chivi.* Members of the *chivi* group in South America have brown irides, a feature shared by immatures of *V. o. olivaceus.* This fact suggests that the developmental pathway leading to red irides in adult *V. o. olivaceus* was switched off during the differentiation of the stock that led to *chivi.* Brown eyes in adults of the latter taxon may be thought of, therefore, as a paedomorphic character. Welty (1982:554) cites examples of colonization and establish-

ment by wintering individuals of other species, thus our suggestion of this phenomenon in vireos is not novel.

Barlow (1980:103) speculated on the origin and phyletic history of "proto-*Vireosylva*" and one of its branches, the "*V. olivaceus* subspecies complex." He proposed that the proto-*Vireosylva* lineage originated in Middle America and subsequently sent a segment into South America in the late Tertiary. There it diversified and eventually gave rise to progenitors of the *V. olivaceus* group. Early representatives of the *V. olivaceus* complex then spread northward in waves, into the Caribbean through the Lesser Antilles and from the mainland of Middle America, leaving proto-*V. magister* and *V. altiloquus,* and continued into North America. Although Barlow does not hypothesize details of branching of forms in the *V. olivaceus* subspecies complex, we interpret his scenario to imply that the South American representative (*V.* "*chivi*") is oldest, the Middle American form (*V. flavoviridis*) is of intermediate age, and the North American component (*V. olivaceus* sensu stricto) is youngest.

The new genetic data offered here, however, do not support Barlow's suggested phyletic history of the *V. olivaceus* group. Instead of being intermediate in age, *V. flavoviridis,* based on its significant genetic differences, is probably the oldest of the three taxa. We feel that the steady, time-dependent accumulation of more allelic changes in *V. flavoviridis* than in *V.* "*chivi*" and *V. olivaceus* verifies the greater age of the former taxon. We emphasize, however, that despite our reliance on a genetic explanation, we still are presenting only a partial analysis of branching patterns in this complex of *Vireo.* A complete understanding of phylogenesis in *V. olivaceus* and its relatives will be possible only when electrophoretic data for *V. altiloquus, V. magister,* and perhaps other forms are available for comparison.

SUMMARY

Using starch gel electrophoresis, we assessed genetic distances among samples of the Red-eyed Vireo (*Vireo olivaceus*), the Yellow-green Vireo (*V. flavoviridis*), and the "Chivi" Vireo (*V.* "*chivi*"). Tissues from a Rufous-browed Peppershrike (*Cyclarhis gujanensis ochrocephala*) provided an outgroup comparison. The three complexes of *Vireo* have been treated in the past either as a single species or as three separate species.

Thirty-eight genetic loci were scored. The Red-eyed and "Chivi" vireos are very similar genetically (Nei's $D = 0.014$). In contrast, these two forms differ strikingly from the Yellow-green Vireo (Nei's $D = 0.177$ and 0.176, respectively). Several branching methods (UPGMA, WPGMA, Wagner Tree and F-M Tree) gave congruent results on relationships. These data support the position that the Red-eyed and "Chivi" vireos are conspecific. The Yellow-green Vireo, however, clearly deserves full species status.

The genic data suggest that the clade leading to *Vireo olivaceus-flavoviridis*-"*chivi*" split from *Cyclarhis* at approximately 13 MYBP. Ensuing separation of *V. flavoviridis* from *V. olivaceus*-"*chivi*" occurred at about 4.6 MYBP. The division of North American *V. olivaceus* from its South American relatives in the "*chivi*" complex occurred approximately 370,000 years ago, during the Pleistocene. We speculate that "*chivi*" arose from wintering individuals of *V. olivaceus* that failed to return to North America.

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COLOR PLATE

The Frontispiece painting of *Tangara meyerdeschauenseei* has been made possible by an endowment established by George Miksch Sutton (1896–1982). The painting is by J. P. O'Neill.

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NORTHERN CARDINAL SONG IN THREE FOREST HABITATS IN EASTERN TEXAS

Mary E. Anderson and Richard N. Conner

Development of song dialects is influenced by (1) the morphological ability of birds to vary their song (Lanyon 1960); (2) the amount of gene flow between populations (Handford and Nottebohm 1976); (3) contrast reinforcement, the conveyance of specific information against a background of many other sounds (Konishi 1970); and (4) social adaptation, a form of modified behavior in which birds copy songs of their conspecific neighbors in response to social interactions (Payne 1981). Although Treisman (1978) theorized that dialects may help to establish and maintain relatively isolated populations, investigators do not agree on a single functional explanation for the existence of song dialects (Hartshorne 1956, Krebs 1977).

Biologists have begun to study the relationships between songs of birds and the efficiency of sound transmission through different acoustic environments (Ficken and Ficken 1962, Morton 1975, Wasserman 1979). Hansen (1979) suggested that young males selectively learn those song elements with acoustic properties that suffer the least amount of distortion during transmission. Acting as very sensitive receivers, young birds would preserve only those sounds which were best adapted for the particular acoustic environment in which they were raised. Gish and Morton's (1981) work on Carolina Wrens (*Thryothorus ludovicianus*) supports Hansen's hypothesis concerning vocal learning in birds. They determined that wren songs transmitted longer distances and retained acoustical properties better when propagated in their native localities than in other habitat conditions. As there is a significant difference in the attenuation rates of the same signal in different environments, the environment itself may be operating as a "filter" between sender and receiver, preventing a bird from copying those sounds which are quickly lost or distorted. Morton et al. (in press), however, recently reported that wrens can reproduce some songs in an undegraded form that they have only heard in degraded form. Morton (1982) advanced a "ranging hypothesis" that suggests that male birds learn the undegraded form of a neighbor's song in order to tell the distance of the singing neighbor. The amount of degradation in the song would help a male determine distances more accurately and know when to challenge if the singer is near and ignore him if far enough away.

Our study examined vocal patterns of three populations of Northern Cardinals (*Cardinalis cardinalis*) in eastern Texas. Our objectives were

to (1) examine differences in the repertoire size and syllable types of the three populations, (2) analyze and compare the morphology of the syllable types, and (3) note trends in acoustic structure and use in different vegetation.

STUDY AREAS

Three relatively homogeneous pine-hardwood stands in the Angelina National Forest were selected as study sites. The three stands were approximately 4.5 km from each other and ranged from mesic to xeric sandy uplands. No major geographical or biotic barriers existed between the sites. They differed primarily in age class of pines and the density of midstory and understory foliage (Ehrhart 1981).

Study area A was a pine sapling stand approximately 18 years old. The small, closely spaced pines characterizing this area averaged 10 m in height. A thick shrub layer occurred between 2 and 4 m. The dominant species of trees in terms of relative abundance were shortleaf pine (*Pinus echinata*), blackjack oak (*Quercus marilandica*), post oak (*Q. stellata*), and longleaf pine (*P. palustris*).

Study area B was a pine pole stand approximately 43 years old. The larger pines and hardwoods (31–45 cm diameter at breast height) formed a canopy at 25 m. A very thin shrub layer was measured as high as 3 m. Loblolly pine (*P. taeda*), shortleaf pine, and longleaf pine were the dominant species of trees.

Study area C, a sawtimber stand aproximately 59 years old, had an upper tree canopy between 17 and 29 m. Midstory foliage of small diameter hardwoods was present between 7 and 12 m. Due to this extensive overstory cover, the understory was relatively sparse with few shrubs and minimal ground cover. The dominant species of trees were shortleaf pine, post oak, sweetgum (*Liquidambar styraciflua*), and flowering dogwood (*Cornus florida*).

METHODS

A 6-ha grid of ¼-ha plots was marked off to provide reference points when mapping the territories of cardinals. A total of 70 days was spent observing birds between 24 March and 18 July 1979. We visited sites on a rotating basis, usually every 3 days. Territories were determined by noting singing posts of males and those points where fights and chases took place (International Bird Census Committee 1970). Simultaneous bout singing was also used to affirm boundaries between adjacent territories.

The song repertoires of 16 cardinals were sampled: 5 cardinals each in the sapling and pole stands, and 6 cardinals in the sawtimber stand. By plotting the number of new syllables recorded vs total syllables recorded, we estimated that 90 to 110 songs were required to obtain an approximate measure of syllable repertoire. Fewer than 50 songs were recorded for 2 of the 6 cardinals in the sawtimber area. Data collected on these 2 birds were used only when testing for differences among the three populations. Repertoire sizes of one male from the sapling area (N = 73) and one male from the sawtimber area (N = 77) may have been underestimated slightly for between-bird comparisons.

Playback tapes were not used to promote singing. All recordings were made with a Uher 4000 Report L recorder at a tape speed of 19 cm/sec. A 40-cm parabolic reflector was used to focus the sound on a Dan Gibson EPM P-650 electronic microphone. Most recordings were made within 8 m of singing males.

All field recordings were reviewed at ¼ tape speed (4.7 cm/sec), and syllable types were identified. We verified syllable patterns with sonagrams made on a Kay Elemetrics model 7029A Sonagraph using the wide band setting with a frequency range of 80–8000 Hz. We

noted the kinds and numbers of syllables used in each song as well as song length and intersong interval. The last two variables were measured to the nearest 0.1 sec using an electronic stopwatch.

In order to describe syllable structure of each population, a random sample of 100 syllables was taken from each cardinal population. Within each population, an equal number of syllables was sampled randomly for each bird: 20 syllables per bird (5 birds) in the sapling and pole stands, and 25 syllables per bird (4 birds) in the sawtimber stand. Sonagrams were made on all 300 syllables using the wide band filter setting. Seven measurements were taken from these sonagrams: frequency range, frequency modulation, frequency with the greatest amplitude, highest frequency, lowest frequency, syllable duration (sec), and the time between syllables (sec). We also noted the number of elements in each syllable. The first three variables parallel those Morton (1975) used to arrive at his song–habitat correlations.

Frequency modulation of syllables was evaluated as an angular measurement of the rate of frequency change. Each syllable was divided into four equal segments, with five vertical lines; this provided five possible points of intersection with the syllable. At each point, the angle of inclination was measured in degrees with respect to the horizontal axis. Each angle was recorded as an acute angle, without regard for the quadrant in which it fell. Measurements were then totaled, and the average final angle was used as the index of frequency modulation, a measurement of the change in frequency over time.

RESULTS

Vegetation.—Foliage-height profiles were constructed to characterize the physiognomy of each study area (Fig. 1). The sapling stand, the youngest of the three areas, had a very thick understory consisting of numerous woody and herbaceous species, and was the only site that lacked an upper tree canopy. Both of the older stands had sparse understories beneath foliage in the upper and midstory vegetation.

Repertoires.—Thirty-two different syllable types were identified in our study: 23 syllables in both the sapling and pole stands, and 20 in the sawtimber stand. Four of the 11 syllables shared among the three areas were simple, one-element sounds (Table 1). Of the 23 syllables recorded in the sapling stand, 15 were sung by four of five cardinals in the area (Table 1). Syllable repertoires of cardinals averaged 16.4 syllables (range = 9–21) in the sapling stand, 13 (8–17) in the pole stand, and 12.5 (8–16) in the sawtimber stand. Differences in repertoire size among the three areas were not significant (Kruskal-Wallis one-way ANOVA, $P > 0.1$).

The average number of syllables in a song was the most variable song parameter in each study area (Table 2). Of the songs recorded, 65% consisted of two syllables; 33% had just one syllable; the remaining 2% consisted of combinations of three syllables.

Many more syllables were shared among birds in the sapling stand (16.0) than in either the pole (11.4) or sawtimber (11.5) stands. This higher degree of syllable sharing reflected the intensity of matched countersinging and the higher density of cardinals in the sapling stand. Density of cardinal

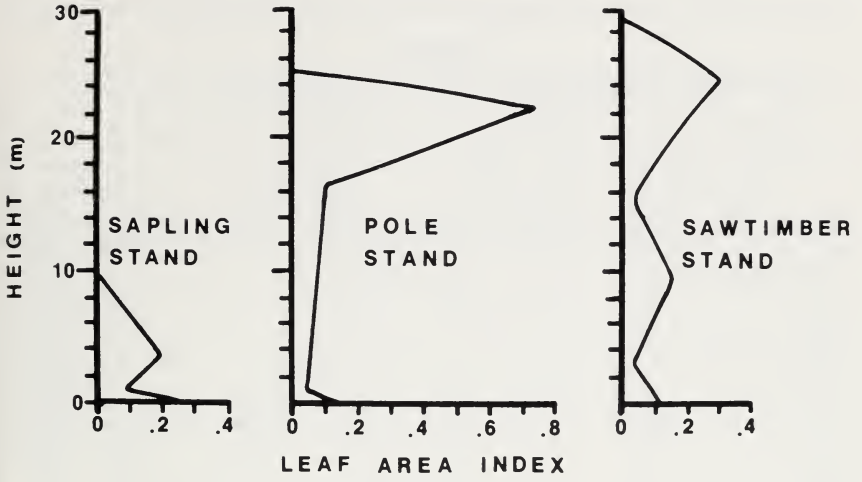

FIG. 1. Vertical foliage profiles of each study area based on foliage density measurements taken at ground level, 1 m, 2 m, 3 m, 7–12 m, 13–20 m, and 20 m (Ehrhart 1981).

pairs was higher in the sapling stand (1.05 pairs/ha) than in the pole (0.94 pairs/ha) or sawtimber (0.88 pairs/ha) stands.

The greatest amount of syllable sharing (percent overlap, Schoener 1970) occurred within each area (Sapling: $\bar{x}$ syllable sharing = 39%, Pole: $\bar{x}$ = 44%, Sawtimber: $\bar{x}$ = 38%) (Table 3); percent overlap was greatest between immediate neighbors. Between areas, substantial syllable sharing was also noted in the repertoires of birds from the pole and sawtimber stands ($\bar{x}$ = 28%). Overlap in syllable usage between cardinals in the sapling and sawtimber stands averaged 24%; between birds in the sapling and pole stands overlap averaged 21%.

Cluster analysis on syllable types (Dixon and Brown 1979) was used to group individual cardinal repertoires (Fig. 2). At the level of three main clusters, syllable usage successfully segregated all but one of the repertoires according to area (cardinal A-5 from the sapling stand). The increase in amalgamation distance obtained by forming two clusters (the sapling cluster and the pole-sawtimber cluster) from the three clusters was 1.8 units (Fig. 2). A 3.4 increase was needed, however, to form the final cluster consisting of all three areas, suggesting again that songs in the pole and sawtimber stands were more similar to each other than they were to songs in the sapling area.

A three-group stepwise discriminant function analysis (DFA) on syllables and song variables (Table 1 and 2) using Rao's V to maximize

TABLE 1

THE NUMBER OF CARDINALS IN EACH AREA THAT USED A PARTICULAR SYLLABLE TYPE AND NUMBER OF SYLLABLES RECORDED

Syllable type	Area						Total	
	Sapling		Pole		Sawtimber			
	No. males	No. recorded	No. males	No. recorded	No. males	No. recorded	No. males	No. recorded
A (3)[a]	4	89	1	2			5	91
B (3)	5	176	1	2			6	178
C (3)	4	65	3	120	1	2	8	187
D (3)	4	157					4	157
E (2)	4	92	4	46			8	138
F (1)	4	86	5	121	3	125	12	332
G (1)	5	189	5	45	2	34	12	268
H (26)	5	101	5	15	2	21	12	137
I (2)	1	10	5	193			6	203
J (3)	4	74					4	74
K (3)	4	74					4	74
L (2)	4	52					4	52
M (2)			3	22	2	123	5	145
N (3)	2	63					2	63
O (2)			1	1	2	67	3	68
P (1)	2	30	4	51	3	134	9	215
Q (2)	5	102	2	53	4	76	11	231
R (1)					4	86	4	86
S (3)			5	82	1	14	6	96
T (1)			2	74	3	174	5	248
U (3)			1	3	3	145	4	148
V (2)	4	114	3	46	3	61	10	221
W (2)	3	35	4	118	3	89	10	242
X (2)			1	10	3	73	4	83
Y (2)	4	23	1	8	3	53	8	84
Z (3)	1	40					1	40
AA (1)	3	97	1	1	1	14	5	112
BB (1)			3	233	2	14	5	247
CC (2)	3	48	1	26	1	35	5	109
DD(2)	3	36					3	36
EE (2)					4	70	4	70
FF (2)	4	127			4	163	8	290

[a] Number in parenthesis indicates the number of structural elements in each syllable type.

separation of areas was used to test the integrity of the three dialects identified by cluster analysis (Dixon 1977). Group separation was highly significant ($P < 0.001$); 87.4% of all the songs were correctly classified according to area. Syllables BB, I, and C were the first variables to enter

TABLE 2
STRUCTURE OF CARDINAL SONGS IN THREE FOREST STANDS IN EASTERN TEXAS

	Sapling	Pole	Sawtimber
No. of birds	5	5	6
No. of songs	947	855	809
Song duration (sec)	3.56 ± 0.4 (36)[b]	2.67 ± 0.04 (41)	3.27 ± 0.05 (39)
No. of syllable types per bird[a]	16.4 ± 2.01 (27)	13.0 ± 1.61 (28)	12.5 ± 2.06 (33)
No. of syllables per song	11.28 ± 0.21 (57)	7.88 ± 0.15 (55)	9.49 ± 0.18 (52)
No. of syllable types per song	1.99 ± 0.03 (45)	1.57 ± 0.02 (38)	1.86 ± 0.02 (28)

[a] Calculations based on birds with 50 or more recorded songs.
[b] Mean ± SE (CV).

the analysis while song length was the fourth. Pearson correlations between the original variables and the first and second discriminant functions revealed that syllables T, B, M, D, BB, FF, and I, as well as song length and the number of syllable transitions per song, were important in separating cardinal song in the three study areas. All of these syllables were used commonly in one or two of the areas (Table 1).

Syllable characteristics.—Northern Cardinal songs ranged from 1000 to 7000 Hz. The mean frequency range for 100 randomly selected syllables in each area was considerably smaller: 3050 Hz in the sapling stand, 2760 Hz in the pole stand, and 2400 Hz in the sawtimber stand (Table 4). For each of these frequency ranges, the mean lower frequency was approximately 1400 Hz (ANOVA, $N = 300$, $P > 0.50$); the frequency with most amplitude was about 2100 Hz for all areas.

Stepwise DFA (using Rao's V to maximize separation of groups) was used to detect differences in the physical nature of cardinal syllables among the study areas. Frequency modulation was the most important variable in the discrimination among syllables in study areas. A one-way ANOVA ($P < 0.01$) and Duncan's New Multiple Range Test ($P < 0.01$) indicated that, with respect to frequency modulation, syllables recorded in the pole and sawtimber stands were similar, but that syllables from the sapling stand were significantly different (Table 4). Cardinals in the pole and sawtimber stands used syllables with relatively "flat" configurations, i.e., less frequency modulation than those used by cardinals in the sapling stand. Although syllable H (a terminal trill note) was used in the first two areas, it was seldom heard and rarely recorded.

Factor analysis (Dixon and Brown 1979) revealed a negative relation-

TABLE 3

OVERLAP MATRIX OF CARDINAL SYLLABLE TYPES IN THREE TIMBER STANDS IN EASTERN TEXAS

	Sapling					Pole					Sawtimber			
Bird	Bird 2	Bird 3	Bird 4	Bird 5	Bird 7	Bird 18	Bird 19	Bird 21	Bird 22	Bird 23	Bird 10	Bird 13	Bird 15	Bird 16
Sapling														
2	—	0.49[a]	0.39	0.34	0.54	0.40	0.08	0.28	0.26	0.35	0.30	0.21	0.24	0.31
3	13[b]	—	0.56	0.19	0.46	0.11	0.02	0.13	0.12	0.16	0.18	0.10	0.17	0.26
4	14	15	—	0.14	0.46	0.15	0.04	0.14	0.18	0.14	0.20	0.16	0.12	0.23
5	7	9	6	—	0.35	0.27	0.11	0.18	0.15	0.20	0.19	0.12	0.22	0.36
7	15	16	15	8	—	0.30	0.20	0.28	0.41	0.47	0.44	0.20	0.33	0.45
Pole														
18	10	10	8	7	11	—	0.25	0.42	0.24	0.35	0.34	0.31	0.25	0.37
19	4	3	3	3	5	8	—	0.53	0.69	0.44	0.33	0.09	0.22	0.14
21	8	8	6	5	10	13	8	—	0.48	0.34	0.47	0.24	0.29	0.28
22	6	6	5	4	9	9	7	11	—	0.66	0.49	0.13	0.24	0.31
23	6	8	5	4	9	8	5	10	9	—	0.33	0.08	0.25	0.35
Sawtimber														
10	9	8	8	4	10	9	4	10	8	7	—	0.28	0.57	0.44
13	4	4	4	1	5	6	2	4	2	1	7	—	0.20	0.44
15	6	6	5	4	6	6	4	8	4	4	9	4	—	0.37
16	7	8	7	2	9	9	3	10	6	7	13	7	7	—

[a] Percent overlap (Schoener 1970) expressed in decimal form appears above the diagonal.
[b] Numbers below the diagonal indicate how many syllable types were shared between two individual cardinals.

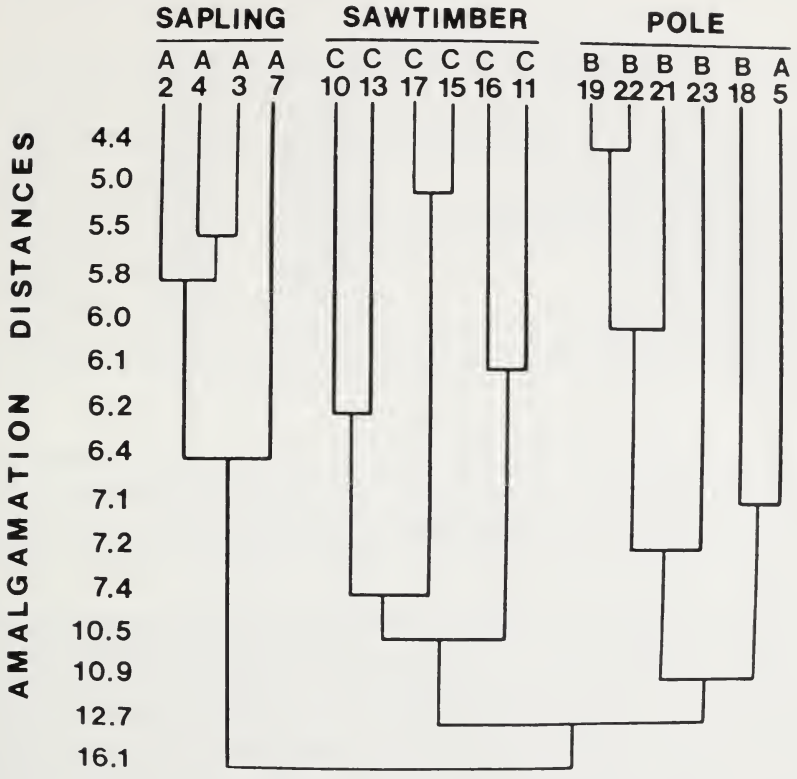

FIG. 2. Dendrogram of three groups formed by cluster analysis based on how many times each syllable type was recorded for each bird. Case labels correspond to the area and territory of each bird; amalgamation distances for each cluster appear to the left of the dendrogram.

ship between frequency modulation and syllable length ($r = -0.62$, $P < 0.01$). As frequency modulation decreased and syllable length increased, syllables became relatively "flat."

Four factor analyses were calculated on syllable structure (same variables as in Table 4): one to describe the variance in syllable structure for the three areas combined, and one for each area separately. The composite factor analysis explained 76.1% of the total variation among the three areas with three factors (Table 5). Its first and most important factor, a general frequency factor, explained 34.3% of the observed variation. Three of the four frequency measurements had the highest factor loadings, with highest frequency and frequency range contributing the most. The second factor explained 27.6% of the variation; it defined a reciprocal relationship

TABLE 4

STRUCTURE OF 100 RANDOMLY SELECTED SYLLABLES FROM EACH CARDINAL POPULATION

	Sapling	Pole	Sawtimber
Frequency range (Hz)	3048 (35)[a]	2760 (45)	2408 (38)
Frequency modulation (degree)	51 (28)	44 (31)	43 (29)
Frequency with greatest amplitude (Hz)	2139 (17)	2197 (12)	2078 (16)
Highest frequency (Hz)	4410 (24)	4247 (30)	3827 (27)
Lowest frequency (Hz)	1385 (14)	1387 (14)	1419 (17)
Syllable duration (sec)	0.23 (73)	0.25 (67)	0.28 (60)
Time between syllables (sec)	0.12 (72)	0.15 (71)	0.13 (50)
No. of elements in syllable	2.34 (107)	1.93 (36)	1.68 (43)

[a] Mean (CV).

between song length, intersyllable interval, and frequency modulation. This factor, therefore, would describe the general configuration of the syllable. The third factor, explaining 14.2% of the variation, specified the number of elements in a syllable, an indication of the complexity of the syllable.

The results obtained in the factor analyses for the pole and sawtimber stands were virtually identical to those discussed above, the only difference being that the pole stand lacked a third factor (Table 5). The three factors derived for the sapling stand, however, were quite different, primarily because the first factor identified syllable configuration (frequency modulation and syllable length), not frequency, as the most variable characteristic.

DISCUSSION

Although Northern Cardinal dialects have been described previously (Lemon 1965, 1966, 1975), they have never been reported for populations separated by very short distances. In our study, significant differences in syllable usage were detected in the songs of three populations located within 4.5 km of one another. Cluster analysis identified three dialects and indicated a rather strong similarity in the dialects for the pole and sawtimber stands (see amalgamation distances, Fig. 2). This high degree of similarity was also noted in the amount of syllable sharing that occurred between those two areas (Table 3).

Syllable sharing occurred both within and among the three areas. In each area, the repertoires of males from adjacent territories were more similar than those of distant neighbors. This pattern of syllable sharing is quite common among songbirds with geographic dialects (Kroodsma 1975, Payne and Payne 1977, Jenkins 1978) and is thought to result from

TABLE 5

VARIMAX ROTATED FACTOR MATRIX FOR EIGHT SYLLABLE CHARACTERISTICS[a]

	Factor										
	All three areas			Sapling			Pole		Sawtimber		
	I	II	III	I	II	III	I	II	I	II	III
Frequency range	0.96	−0.11	−0.01	0.08	0.94	0.22	0.90	−0.18	0.96	−0.08	0.17
Frequency modulation	0.13	−0.84	0.01	−0.93	−0.07	0.12	0.18	−0.98	0.14	−0.82	0.18
Freq. with most amplitude	0.53	0.21	0.11	0.02	0.19	0.55	0.77	0.01	0.54	0.45	−0.34
Highest frequency	0.99	−0.01	0.02	0.10	0.92	0.38	0.95	−0.09	0.98	0.07	0.17
Lowest frequency	0.24	0.43	0.14	0.28	0.01	0.59	0.16	0.44	0.43	0.52	0.02
Syllable duration	0.29	0.70	0.47	0.78	−0.12	0.36	0.59	0.62	0.28	0.85	0.12
Time between syllables	−0.04	0.75	−0.17	0.64	0.00	0.30	−0.13	0.59	−0.17	0.61	−0.48
No. of elements	0.01	−0.01	0.63	0.15	−0.34	0.17	0.58	0.17	0.08	−0.02	0.59
% variance explained	34.3	27.6	14.2	35.1	25.8	14.1	41.7	28.2	39.1	29.7	13.7
Cumulative %	34.3	61.9	76.1	35.1	60.9	75.0	41.7	69.9	39.1	68.7	82.4

[a] Factor loadings given for each variable analyzed according to area.

frequent interactions (learning) between neighboring territorial males. Payne (1982) suggested that song matching is a form of deceptive mimicry where young males may copy the songs of previous or established males to enhance their own likelihood of success when setting up a territory. McGregor and Krebs (1984), however, suggested that the use of known songs to exchange information on distances between male birds is perhaps a more advantageous reason for song matching.

While studying various song dialects among Darwin's finches, Bowman (1979) found a strong correlation between song bandwidth and the acoustical conditions in the environment of each species. In our study, Northern Cardinals in the sapling stand sang a wider range of frequencies than did those in the sawtimber stand. This supports what Morton (1975) had documented earlier: forest-inhabiting birds use narrower frequency ranges than do birds inhabiting more open areas.

For all three populations, the frequency with most amplitude was about 2100 Hz. Such frequencies are within the range of frequencies (2000–8000 Hz) that distort the least over long-distance transmission (Richards and Wiley 1980); however, extreme attenuation results whenever frequencies less than 2000 Hz are produced just above ground level (Marten et al. 1977). As Northern Cardinals typically sang from high perches, this particular acoustical problem may have been eliminated.

In tropical forest environments, bird sounds typically are pure and tonelike with very little frequency modulation (Morton 1975). Because older forests have closed tree canopies, signals with amplitude modulation and repetitive frequency modulation (trills) transmit poorly due to the echoes and reverberations generated by the forest canopy (Richards and Wiley 1980). This is especially true for long-range communication. It would be disadvantageous for cardinals in either the pole or sawtimber stands to use syllables with significant frequency modulation. In contrast, birds living in relatively open areas can enhance message encodement (using frequency and amplitude modulation) in songs transmitted over long-distance with less risk of distortion (Morton 1975, Richards and Wiley 1980).

The foliage density profiles constructed for each of the three study areas indicated a similarity in the physiognomy of the pole and sawtimber stands (Ehrhart 1981) (Fig. 1). Both had a complete canopy that would cause excessive reverberation in sounds with extensive frequency modulation. In contrast, the sapling stand had dense understory vegetation, no canopy, and several large open areas. Because cardinals in this area typically sang from perches 6–8 m high in the upper branches of the young pine trees, little foliage was present to distort the acoustic signals. In this environment, cardinals used syllables with frequency modulation more

than did cardinals in the pole and sawtimber stands, as predicted from Richards and Wiley (1980).

Nuechterlein (1981) found that auditory signals helped maintain the two color phases of the Western Grebe (*Aechmophorus occidentalis*) even in sympatric populations. He considered this to be a learned behavior operating singly on individuals. The selective advantage of this possible isolating mechanism in pair formation would be recognition of individuals similarly adapted to a particular habitat condition.

SUMMARY

Song repertoires of Northern Cardinal (*Cardinalis cardinalis*) populations in neighboring sapling, pole, and sawtimber stands in eastern Texas were tape recorded during the 1979 breeding season. Cardinals in each area used different syllable types and sang songs of varying duration and complexity. Cluster analysis and discriminant function analysis identified three distinct dialects, one for each of the three study areas. Cardinals in the sapling stand used a wider range of frequencies than did those in the sawtimber stand. Cardinals in the pole stand used a range of frequencies intermediate in size to that of either the sapling or sawtimber stands. For all three populations, the frequency with greatest amplitude was about 2100 Hz, a low frequency that carries better than high frequencies over long distances. In the stand that lacked a closed canopy, cardinals typically used syllables with considerable frequency modulation; however, in the two older stands cardinals seldom used extensive frequency modulation in their songs. Differential singing behavior of this nature probably enhances long-distance communication by minimizing excessive reverberation from canopy foliage. We suggest that some of the differences in syllable structure noted between the three cardinal dialects may be the result of selective pressures exerted by the acoustics of the environment.

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REPRODUCTIVE ENERGETICS OF BLUE-EYED SHAGS IN ANTARCTICA

Neil P. Bernstein and Stephen J. Maxson

Time and energy budget estimates have been used to measure parental investment of birds despite the difficulties of comparing the consequences of proximate energy allocation on future reproductive success (Walsberg 1983). These estimates are popular, in part, because they encompass the risks, costs, and benefits of parental investment simultaneously, all of which must be balanced if parents are to achieve maximum lifetime fitness (Trivers 1974, Patterson et al. 1980, Wittenberger 1982).

Measuring energy expenditure in the field is usually accomplished by converting the bird's behavior and thermal relation to the environment to energy expended. Although these techniques have been criticized for their inaccuracy (Weathers and Nagy 1980, Williams and Nagy 1984), with adequate sampling, most error in energy estimates results from the use of somewhat arbitrary conversion factors expressed in multiples of standard metabolic rates. Ettinger and King (1980) have demonstrated that inaccuracies in estimating individual components of a time budget resulted in little variation of daily energy expenditure if no large errors were made in estimation of energetically costly activities or activities that consumed large amounts of time (see also Mugaas and King 1981). Even so, by using the same conversion factors for all individuals, individual comparisons should be valid even if they do not represent accurate energy expenditures.

We here report time and energy budget estimates of individual Blue-eyed Shags (*Phalacrocorax atriceps bransfieldensis*) in Antarctica. We asked two questions: (1) What are the patterns of time and energy allocation between sexes, and (2) does each sex of these monogamous birds equally allocate time and energy into reproduction?

METHODS

The study area and methods are partially described in Bernstein and Maxson (1984). For coherency, parts of the methods from that publication are repeated.

We collected 3198 bird-h of time budget data from 15 January 1979 to 1 April 1979 and from 23 September 1979 to 15 March 1980 at a colony of Blue-eyed Shags on Shag Island, 5 km southwest of Palmer Station, Anvers Island, Antarctica (64°46′S, 64°03′W). There were 485 nests on 31 December 1978, and 326 on 19 December 1979. During sample days, we observed 2–10 nests simultaneously every 30 sec, at the tone of a metronome (see Wiens et al. 1970), either from dawn to dusk or for 24 h during periods of continuous daylight. All statistical calculations were based upon these nests, which were observed for continuous

TABLE 1
AVERAGE MONTHLY WEATHER DATA AT PALMER STATION

Month/year	Temperature (°C)	Percent cloud cover	Wind speed (knots)
Jan 1979	1.85 ± 0.20[a]	82.9 ± 3.14	6.73 ± 0.81
Feb 1979	1.35 ± 0.24	91.8 ± 2.20	9.98 ± 1.06
Mar 1979	0.73 ± 0.16	94.5 ± 1.37	8.31 ± 0.78
Sep 1979	−4.96 ± 0.53	89.3 ± 2.37	12.13 ± 1.29
Oct 1979	−3.58 ± 0.36	93.9 ± 2.00	11.34 ± 1.16
Nov 1979	−0.44 ± 0.31	90.0 ± 2.34	6.22 ± 0.65
Dec 1979	1.65 ± 0.19	83.7 ± 3.14	4.88 ± 0.60
Jan 1980	1.86 ± 0.17	78.7 ± 3.11	5.03 ± 0.56
Feb 1980	2.52 ± 0.17	85.0 ± 2.89	5.95 ± 0.68

[a] Mean ± SE.

lengths of time (see Table 2 for sample sizes), but time budget graphs reflect all nests observed. In addition, 84 bird-h, 64 of which were filmed at one nest for 32 continuous h, were obtained using a Super-8 movie camera timed to expose one frame approximately every 30 sec. No observations were conducted during heavy rain or during winds greater than 30 knots. These conditions were infrequent (Table 1). Blinds, 10–25 m from the birds, concealed us after September 1979, but the shags seemed undisturbed unless we were close to their nests. Shags were captured with short-handled nets, examined for molt, weighed with a 5 kg Pesola spring scale, and banded with stainless steel bands. Birds under observation were color banded. Adult shags were sexed by body and bill size and by vocalizations (Bernstein and Maxson 1984, Shaw 1984).

Behavioral activities included preening, resting, standing, flying, walking, nest building, incubation, brooding, courtship, pairbond maintenance, copulation, chick feeding, chick preening, face-offs, gathering nest material (algae) nearby (Bernstein and Maxson 1982a), foraging, swimming above water, diving (and swimming underwater), and bathing. Shags were assumed to be foraging when absent from the nest or from the vicinity of the colony.

Blue-eyed Shags maintained rigid, sexually distinct, activity patterns throughout the colony except during periods of severe weather or extensive ice cover (Bernstein and Maxson 1984). The only other disruptive factor was prey piracy by South Polar Skuas (*Catharacta maccormicki*) early in the breeding season (Maxson and Bernstein 1982). Therefore, time budget data collected on the observed pairs probably applied to most of the colony.

Data were grouped by sex for each of the following stages of the breeding cycle: prelaying, laying–incubation, brooding, and fledging periods. Criteria used to determine these stages are described in Bernstein and Maxson (1984).

Pack ice limited travel to the island during early stages of the breeding cycle and the early and middle chick rearing periods, and data for these brood periods are few.

To determine climatic variables affecting energetics of thermoregulation by gular fluttering (a thermoregulatory behavior), we observed 10 nests during one 24-h period. Every 15 min, we recorded the proportion of shags gular fluttering, wind speed with a hand-held anemometer, relative humidity with a sling psychrometer, air temperature at nest level with a thermistor, and relative brightness with a light meter in a single lens reflex camera. Daily weather data were also collected at 08:00, 14:30, and 20:00 at Palmer Station.

Calculation of Daily Energy Expenditure.—Daily Energy Expenditure (DEE) was calcu-

lated as multiples of standard metabolic rates (SMR). Ricklefs and Matthew (1983) measured oxygen consumption for six Blue-eyed Shags and found that SMR was about twice that predicted by Lasiewski and Dawson's (1967) equation. This resulted in a SMR of 60.13 kJ/h for males and 53.57 kJ/h for females.

The following conversion factors were used: night and daytime resting (1.2 × SMR) (King 1974), standing (1.25 × SMR) (Aschoff and Pohl 1970), preening and preening chicks (2.5 × SMR) (Custer and Pitelka 1972), incubating (1.25 × SMR) (King 1973, Walsberg and King 1978), brooding Early chicks (1.25 × SMR) (this study), brooding Middle chicks (1.2 × SMR) (this study), nest building, walking, feeding chicks, and face-offs (3.0 × SMR) (Orians 1961, King 1974), pairbond maintenance (3.0 × SMR), courtship (3.5 × SMR for males, 3.0 × SMR for females) (Orians 1961 and this study), foraging (1.8 × SMR) (see below), bathing (10 × SMR) (this study), flying (15.2 × SMR) (King 1974), and gathering nest material (5.9 × SMR) (see below). The DEE was calculated for each bird and averaged to obtain a mean DEE for each sex during each breeding period.

Feather replacement costs energy (King 1974, Dunn 1979, Mugaas and King 1981, Walsberg 1983). Molt, however, was not frequent during the breeding season (Bernstein and Maxson 1981), and was not included in estimation of DEE.

Energy cost of foraging involved the following: flight speed, distance traveled, and behavior while away from the nest. Blue-eyed Shags took 1.15 min ± 0.08 [SD] (N = 13) to travel 1 km during normal flight in winds under 10 kmh, and, therefore, flew at approximately 52 kmh. It was not possible to follow shags on foraging flights, but judging from the direction taken on most days, knowledge of ice-free habitats, and location of other shag colonies, a conservative estimate of 10 km was made for average distance traveled to forage, and a 20-km flight was added to the daily time budget. For comparison, DEE was also calculated with a 30-km and 40-km roundtrip. Because shags usually foraged beyond permissable travel boundaries around the station, our time budget data on foraging behavior only totaled 11.5 h over 5 days on 1–4 birds at a time. Larger foraging flocks were observed early in the breeding season, but no time budget data were collected on these birds.

The costs of swimming and diving were estimated from other studies. Although Kanwisher et al. (1981) reported an immediate 50% tachycardia and an increase in breathing rate as Double-crested Cormorants (*P. auritus*) surfaced after diving, no difference was noted in the heart rate of shags between normal above water swimming and diving. Therefore, swimming and diving were given the same energy conversion values based on Prange and Schmidt-Nielsen's (1970) estimate of above water swimming in the Mallard (*Anas platyrhynchos*). Because time spent in increased oxygen consumption during the interdive occurred for only an extremely small proportion of the day, it was not accounted for in the energy budget.

Energetic costs of gathering nest material, which involved males only, encompassed several separate behavioral patterns (Bernstein and Maxson 1982a, 1984). Males flew to nearby shallow water and collected benthic algae during short dives. Distance to the algae beds was approximately 0.4 km, and the flight time for a round trip was 0.9 min. Average time for a complete trip was 4.4 min ± 1.8 (N = 47) with time used in diving making up the difference between total trip time and round-trip flight time. When appropriate conversion factors are applied, energy cost of gathering nest material was 5.9 × SMR. Shaw (pers. comm.) has noted females also gathering nest material, but we did not.

The cost of egg production must be added to the energy budget of females during prelaying and laying–incubation periods. Additional data to make this calculation were collected by Shaw (1981, 1984), who had access to a large, banded colony of Blue-eyed Shags.

Three-egg clutches were most common (2.5 ± 0.6, N = 811 nests, this study; 2.31–2.84,

N = 1230 from 1979–1981, Shaw, in press). Freshly laid eggs were weighed in the field with a 100-g Pesola spring scale. Average egg weight was 59.1 g ± 3.99 (N = 13) for this study; and Shaw (1981), who was able to measure more smaller, third eggs in the clutch, found a mean weight of 54.6 g (N = 623). The combined average egg weight from the two studies was 54.7 g, and this value was used to calculate costs of egg production because it allowed for smaller, third eggs. Shaw (1981) measured the egg-laying interval at 2.59 days (N = 544) for 3-egg clutches, which was the value used in calculations. Two-egg clutches had a longer laying interval (Shaw 1985).

Two freshly laid first eggs were collected and analyzed in an adiabatic oxygen bomb calorimeter. The eggs were oven dried at about 15.5°C and ground to a uniform consistency with a mortar and pestle. The ground egg shell was added before analysis. Ten samples from each egg were tested.

Egg samples averaged 3.85 kJ/g ± 0.40 dry weight or approximately 220 kJ/egg. Assuming a 70% efficiency of production (King 1973), each egg costs about 313 kJ to produce. If approximately 7 days are required for egg production, given the egg-laying interval (above), maximum energy expenditure for a clutch of 3 eggs equals 134 kJ/day during prelay and 139 kJ/day during laying–incubation (see King 1973).

Maximum energy costs of testicular and ovarian development are small (Walsberg 1983). Distributed over an uncertain number of days, energy costs of gonadal growth were assumed to be minimal and were not included in the DEE.

RESULTS

Meteorological data collected in conjunction with gular-flutter patterns revealed no definite trends. Shags tended to gular flutter at temperatures above 2°C and when exposed to bright sun, but some also gular fluttered in misty conditions near 0°C. The only predictable time of gular flutter was at return to the nest from a foraging flight, when the shags were overheated from exertion. Meteorological data collected at Palmer Station indicated that temperature, wind speed, and cloud cover varied little within a month and were similar among months of the breeding season, especially December through March when chicks were present (Table 1).

Observations of shags away from the colony indicated that only 8.4% of the time was spent swimming or diving, and 91.6% of the time was spent preening, standing, or resting on shore. Short flight times between shore and water and vice versa were not accounted for in the estimation of DEE.

Fifteen observations were made of foraging shags for 40 sec–50 min. Dive and interdive times were recorded for either single birds or flocks of up to 84 individuals, which dove synchronously. Dive times ranged from 5 sec to 3.5 min, and interdive times were between 2 sec and 4.3 min. Flocks of over 200 foraging shags were observed in December, and they also remained submerged for up to 3.5 min. It is not known if this foraging tactic was used throughout the breeding season. Lone shags remained submerged for less time than did the majority of shags in a group

(94 sec ± 50.5 [N = 35] and 189.62 sec ± 22.5 [N = 13]; $t = 6.55$, df = 46, $P < 0.001$). Only 4 dives of lone shags exceeded the minimum dive length of 150 sec by groups of shags.

Time budgets.—Most patterns of behavior illustrated in Figs. 1 and 2 are described in Bernstein and Maxson (1982a), and not all of them will be discussed in this paper. A minimum of 9 h of darkness prevented shag activity away from the nest during the prelaying period, and detailed behavioral observations were not possible during this time. Colony checks at night, however, revealed that most nests had pairs present. Therefore, preening, resting, and sitting (pooled together into "Present at the nest" in Fig. 2) comprised over 70% of the 24-h day (Figs. 1, 2). Foraging time could be reduced because shags were not feeding chicks and only had to forage for themselves. Males had to establish a territory and defend the nest site until successfully paired, and after pairing, both sexes had to build and defend a nest against territory usurpers and nest-material thieves (Bernstein and Maxson 1982a). No extra-pair copulation attempts were observed, and mate defense did not appear to be a factor in time allocation. Time spent in courtship, however, indicated the greatest time commitment to pairbond maintenance from prelaying to fledging (Figs. 1, 2).

Males incubated more than females, which spent more time foraging (Figs. 1, 2). Once laying began, nest building activities increased for both sexes, but females spent more time in actual manipulation of nest material, which males continued to gather nearby. During the laying–incubation period, neither sex spent much time at the nest when not incubating, but after the chicks hatched, there was a decrease in foraging for both sexes (Figs. 1, 2). This resulted in an increase in female presence at the nest that was not seen in males because the latter brooded more than females while females rested by the nest (Figs. 1, 2).

Females gradually spent less nonbrooding time at the nest as the breeding season progressed (Figs. 1, 2). Instead of engaging in behavior centered at the nest, females disproportionately increased their foraging time com-

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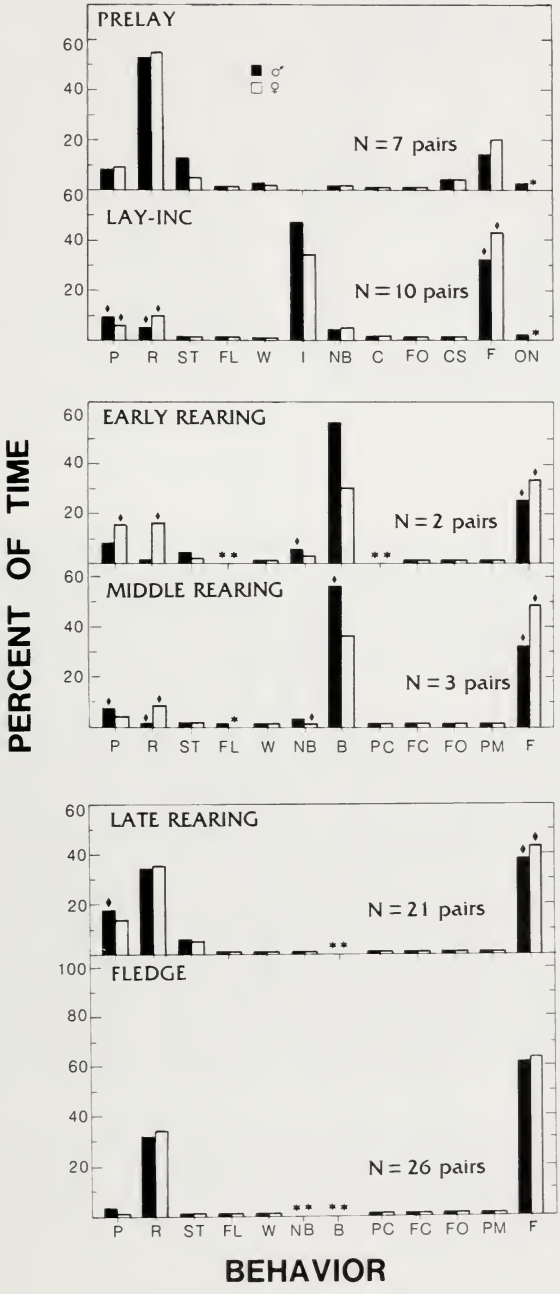
FIG. 1. Time Budgets for Breeding Season. P = Preen, R = Rest, ST = Stand, Fl = Fly, W = Walk, I = Incubate, B = Brood, PC = Preen Chicks, FC = Feed Chicks, NB = Nest Build, C = Copulate, CS = Courtship, F = Forage, FO = Face-off, PM = Pair-bond Maintenance, ON = Gather Nest Material, * = No time spent in this behavior. Diamonds above the bars indicate standard errors between 0.5 and 2.5%; no diamonds above the bars indicate standard errors less than 0.5%. Darkness prohibited observations between 20:00 and 06:00 during prelaying and between 24:00 and 04:00 during the fledging period. Shags were resting at the nest during these times.


PRELAY
♂
♀
N = 7 pairs
LAY-INC
N = 10 pairs
P R ST FL W I NB C FO CS F ON
EARLY REARING
N = 2 pairs
MIDDLE REARING
N = 3 pairs
P R ST FL W NB B PC FC FO PM F
LATE REARING
N = 21 pairs
FLEDGE
N = 26 pairs
P R ST FL W NB B PC FC FO PM F
PERCENT OF TIME
BEHAVIOR

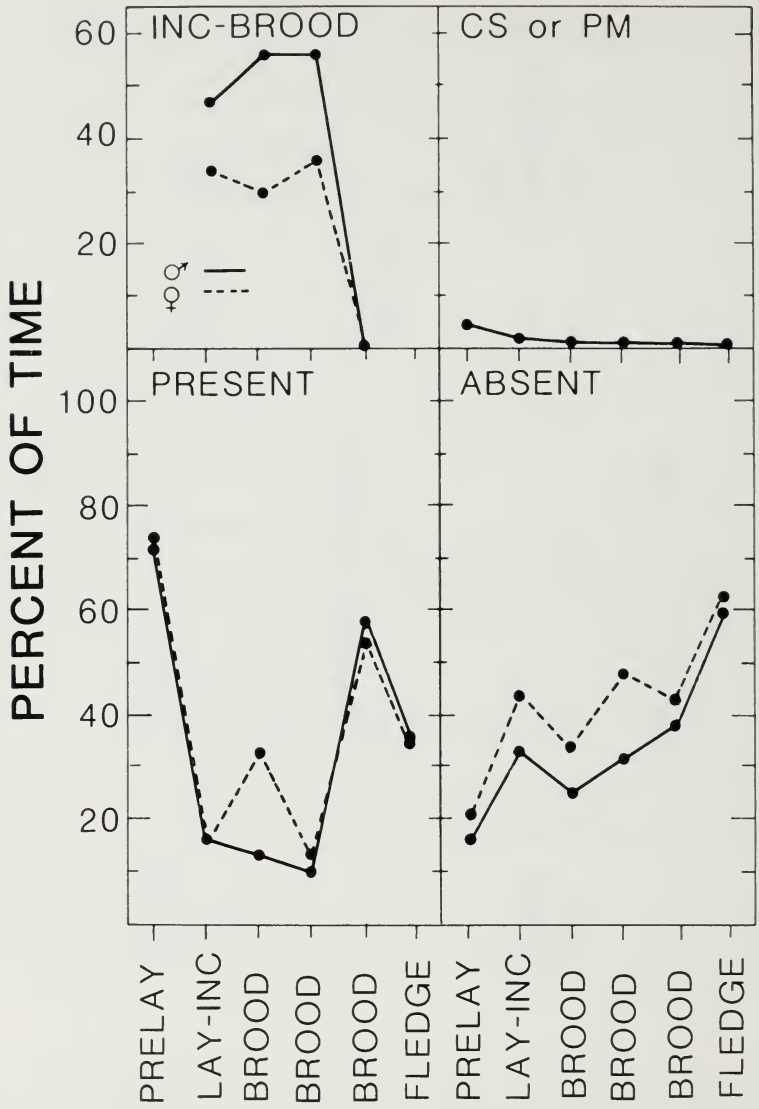


FIG. 2. Percent of time Blue-eyed Shags spent engaged in incubating or brooding, courtship or pairbond maintenance (CS or PM), present at the nest (resting, standing, preening), and absent from the nest. The breeding season is divided into prelaying, laying–incubation, three divisions of the brooding period (early, middle, and late), and the fledging period.

TABLE 2

MEAN DAILY ENERGY EXPENDITURE BY BLUE-EYED SHAGS DURING EACH STAGE OF THE BREEDING SEASON

		Males		Females	
	N[a]	kJ/d	DEE/SMR	kJ/d	DEE/SMR
Prelaying	8	2598 ± 127.6[b]	1.80	2180–2186 ± 22.7[c]	1.70
Laying-incubation	7	2754 ± 43.2	1.91	2384–2390 ± 34.4	1.85–1.86
Early rearing	2	2688 ± 4.3	1.86	2330 ± 75.8	1.81
Middle rearing	3	2574 ± 41.7	1.78	2571 ± 68.0	2.00
Late rearing	12	2844 ± 29.5	1.97	2443 ± 34.0	1.90
Fledging	23	2501 ± 26.3	1.73	2212 ± 8.9	1.72
Mean		2660	1.80	2353–2355	1.83

[a] Number of nests observed for 24 h or from dawn to dusk.
[b] Mean ± SE.
[c] Range given is for minimum and maximum cost of egg production (see text).

pared with the males' increase. Data are too few in early and middle rearing for statistical comparisons, but males and females appeared to feed chicks with equal frequency. Because they were at the nest more, males spent more time in nest maintenance. Shags often preened and rested while incubating or brooding chicks, but this is not illustrated in the figures.

After the chicks grew into the late rearing stage, male and female time budgets became approximately equal as females decreased foraging time and increased nest-centered activites (Figs. 1, 2). Females still allocated more time to foraging than did males, and both sexes foraged more after chick fledging (Figs. 1, 2). Although chicks no longer required brooding during the late rearing period, one parent was always present, perhaps for protection from skuas. This resulted in an increase in presence at the nest for both sexes (Figs. 1, 2). During the fledging period, females usually spent the night on a rocky peninsula near the colony as did some males, probably to escape the vigorous and incessant begging of the chicks. Time on the rocky peninsula accounted for the majority of time represented as "present at the nest" (Figs. 1, 2).

Daily Energy Expenditure.—Daily Energy Expenditures (Table 2) differed between sexes within each period of the breeding cycle (paired t-test, $t = 4.84$, $df = 5$, $P < 0.005$). However, when DEE/SMR ratios were compared (i.e., when weight was accounted for), there were no significant differences even when the maximum cost of egg production was added to the females' DEE (paired t-test, $t = 0.244$, $df = 5$, $P > 0.5$). The DEE/

SMR ratios ranged from 1.70 to 2.00, and are, therefore, among the lower values listed by King (1974) from other avian studies.

The DEE estimates assumed a 20-km round-trip flight for both sexes each day. If, instead, the shags flew 30 km or 40 km, the DEE would be increased about 6.3% or 12.7%, respectively.

We do not believe that our observations altered the normal time budgets. In the austral summer of 1978–79, chick survivorship varied between 44 and 82% in different sections of the colony. The lowest survivorship occurred in sections of the colony that we disturbed during banding, and time budgets were not collected from these birds. Experience in handling the birds lessened disturbance in 1979–80, and undisturbed sections of the colony experienced similar reproductive success (25%) to those in which chicks were weighed and banded and adults were observed. All observed shag colonies on the Antarctic Peninsula experienced low reproductive success that summer (Maxson and Bernstein 1980).

DISCUSSION

The data indicate similarities in time and energy budgets for both sexes of Blue-eyed Shags. The similarities are due, in part, to the similar activity patterns (Bernstein and Maxson 1984), but other factors also affect the energy allocation.

It is difficult to determine how climate affected energy budgets. Berry (1976) found that climatic factors determining onset of gular flutter interacted complexly for the Cape Cormorant (*P. capensis*), and the fact that Blue-eyed Shags showed no clear patterns of gular flutter supports Berry's (1976) observations. Although ambient temperatures affect energy expenditure, Blue-eyed Shags reduced heat loss by various body postures that minimized exposure of fleshy parts and by lack of wing-spreading, possibly to conserve heat (Bernstein and Maxson 1982b). Additionally, Guard and Murrish (1975) reported that the Blue-eyed Shags' high blood viscosity might help to conserve heat, and Dunn (1979) reviewed studies documenting thermoregulatory adaptations of seabirds at high latitudes that reduce energy costs. Therefore, we feel that failure to include energy of thermoregulation will result in minimal error to estimation of DEE, and it should not affect comparisons between sexes substantially.

The high SMR directly affects the energy budget. Ricklefs and Matthew (1983) reviewed studies documenting elevated SMR in high latitude birds, but no explanation was apparent for the trend. The high SMR had several implications for Blue-eyed Shags. Twice the amount of food was necessary to support a Blue-eyed Shag compared with a similarly sized shag in lower latitudes with a lower SRM. Another important consequence was that egg formation became relatively cheap in terms of SMR (see below).

Chicks did not require direct parental attention other than feeding during late-rearing and fledging periods, and adults of both sexes spent equal time in activities (Figs. 1, 2). Montevecchi and Porter (1980) noted constant parental attendance of Northern Gannet (*Morus bassanus*) chicks for protection from antagonistic neighbors, but we did not observe neighboring adults attacking chicks.

It is not known how long parents fed chicks, but Snow (1960) observed 100-day-old chicks of the Shag (*P. aristotelis*) being fed. We observed that recently fledged chicks returned to their nests in all-juvenile groups approximately 1 h before adults. They were then fed by parents, usually in the late afternoon. Juveniles were seen foraging with small groups of adults by mid-February, and most left the colony on foraging flights by early March.

Our data on foraging behavior are similar to those of other studies. Kooyman (1975) reported dive times for this species as ranging between 5 sec and 2.5 min. There was no apparent pattern of dive and interdive times, and shags appeared incapable of a series of lengthy dives, as noted by Croxall and Prince (1980). Van Dobben (1952), Stonehouse (1967), and Siegfried et al. (1976) also observed shag species resting for long periods between foraging bouts as we described, and foraging shags were always observed near land in the Palmer Station area and during R.V. Hero cruises along the Antarctic Peninsula. It is likely that they foraged near the bottom in littoral waters. Shaw (pers. comm.) noted that during October–November 1980, Blue-eyed Shags had to fly 20–25 km each day in order to feed, and the distance traveled daily is probably locally and seasonably different.

Females need additional nutrients during synthesis of eggs (Ashmole 1971), and this may have influenced the slightly greater amount of time female shags foraged during prelaying and laying–incubation. However, given the low energy cost of eggs, this may not be a substantial factor in the energy budget of females.

Most similarities in DEE's between sexes and breeding periods can be explained by similar allocations of time to activities with the same approximate energy costs. About 90% of any day was spent either away from the colony, collectively called foraging, or in nest-related behavior such as preening, resting, standing, incubating, or brooding. All of these activities required similarly low energy output. Male energetic costs of gathering nest material usually equalled or exceeded the females' maximum daily energy costs of egg formation, and this supports the contention that, in some birds, the males' investment in prelaying activities might equal the females' investment in eggs (Gladstone 1979).

Accuracy of our DEE estimations is reduced by our lack of knowledge

of the precise time spent in flight, unknown energy costs of incubation (Walsberg 1983), and our lack of knowledge of the extent of postfledging parental care. Regarding energy for incubation, it seems logical that an incubating shag could have shunted heat to its feet within the shelter of the nest without large energy losses to the environment.

Both sexes of the Blue-eyed Shag, therefore, allocate approximately equal amounts of energy in reproduction. These proximate energy allocations are important because future reproduction and survival can be hindered if adults expend too much energy in a breeding season (Ashkenazie and Safriel 1979, Drent and Daan 1980, Montevecchi and Porter 1980). Although Mugaas and King (1981) found that DEE did not reflect equal energy expenditures between the sexes in the monogamous Black-billed Magpie (*Pica pica*), energy use does reflect equal sharing of reproductive effort in Blue-eyed Shags.

SUMMARY

Time-budget data were collected for Blue-eyed Shags (*Phalacrocorax atriceps bransfieldensis*) in Antarctica and converted to energy budgets to measure proximate energy allocation to reproduction. Time budgets were similar for both sexes, and about 90% of the 24-h activities involved low energy expenditure behavior such as preening, resting, standing, incubating, brooding, and foraging. Birds were classified as foraging when away from the colony, and although the capture of food was energetically costly, most of this time was actually spent preening, standing, or resting on shore between foraging bouts. DEE/SMR ratios were similar for both sexes, indicating equal energy investment in reproduction. Male courtship behavior equalled or exceeded female energy investment in egg production. The additional energy cost of egg production was low because of altricial eggs that were small relative to the weight of females, a 2.59-day laying interval, and the high SMR of the Blue-eyed Shags. Both sexes, therefore, shared equally in the energetics of reproduction.

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INTERSPECIFIC RELATIONSHIPS BETWEEN AMERICAN COOTS AND WATERFOWL DURING FALL MIGRATION

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Interactions between American Coots (*Fulica americana*) and waterfowl during the breeding season are well-documented (Ryder 1959, Nudds 1981). Ducks and coots use similar nesting, feeding, brooding, and loafing sites during the breeding season (Munro 1939, Sooter 1945, Ryder 1959). Coots create potential nest sites, repulse predators, provide predation buffers for ducks (Sooter 1945; Ryder 1958, 1959), and also may destroy eggs and young of other marsh-nesting birds (Munro 1937, Burger 1973, McNicholl 1975). Coots, ducks, and swans often feed cooperatively (Ryder 1959, Anderson 1974, Ryan 1981); and American Wigeon (*Anas americana*) and Gadwall (*A. strepera*) may rob feeding coots (Knapton and Knudsen 1978, Ryan 1981). Interspecific aggression between coots and waterfowl usually occurs when ducks approach coot nests or broods (Ryan and Dinsmore 1979). Despite these interactions, the numbers of duck broods produced in areas in Utah with nesting coots and in areas where coots had been removed were similar (Ryder 1958, 1961). Densities of coots and ducks, and brood counts of coots and ducks for a 26-year period in Saskatchewan also indicated no significant relationship between numbers of coots and waterfowl (Nudds 1981).

Coots and waterfowl from large areas of breeding habitat concentrate on smaller areas during the nonbreeding season (Weller 1975:102). These species may also change diets and habitats during migration and while wintering (Weller 1975). This study documents associations between waterfowl and coots during fall migration and examines feeding and behavioral interactions between coots and waterfowl in mixed flocks. Specifically, we (1) describe temporal and spatial overlap among migrations of coots and waterfowl, (2) present behavioral interactions among species, and (3) document food habits of birds feeding sympatrically during fall migration in Oklahoma.

STUDY AREAS

Field work was conducted on lakes in north-central and eastern Oklahoma. Activities of mixed flocks of coots and ducks were observed on Lake Carl Blackwell, Sooner Lake, Perry Lake, and Lake McMurtry (Payne and Noble counties) (described by Baumgartner 1942, Eddleman et al. 1985), and at Sequoyah National Wildlife Refuge (NWR) (Haskell, Muskogee, and Sequoyah counties). The former are within tallgrass prairie and cross-timber vegetation

types, while the refuge is predominately within the bottomland hardwood vegetation type on Robert S. Kerr Reservoir (Duck and Fletcher 1943). Cultivation of wheat and soybeans for migratory waterfowl is the major land-use on the refuge. Most observations of mixed flocks were made on the upper end of the reservoir and at the mouth of the Canadian River. Cattail (*Typha latifolia*) marshes, beds of Eurasian watermilfoil (*Myriophyllum brasiliense*), open water, beds of water primrose (*Ludwigia repens*), flooded dead timber, and intermittent mud flats were the principal habitats used by coots and ducks.

METHODS

Aerial and ground counts of coots and waterfowl during fall migration determined migration chronology on all lakes but Robert S. Kerr Reservoir. Aerial counts were conducted every five days from September through December 1979 and 1980. The surveys were supplemented with ground counts on Lake Carl Blackwell and Sooner Lake every one to five days from September through December 1979–1981. Temporal overlap was determined by comparison of the chronology of coot migration with the chronology of migration for each species of duck. Coots differed in migration chronology among lakes in the same year and among years on the same lake; thus, chronology data for each lake and year were analyzed separately (Eddleman et al. 1985). To determine correlations among numbers of coots and numbers of ducks, we calculated Spearman rank correlation coefficients (Conover 1980:251), which minimized problems of nonnormal distribution of count data. Dates of counts were used as sample points, and correlation analyses were conducted for all lakes and for Lake Carl Blackwell and Sooner Lake yearly. Significant positive correlations were interpreted as significant overlap in chronology between coots and the species under consideration, and significant negative correlations were interpreted as a lack of significant overlap in chronology.

Given temporal overlap, species may not overlap spatially. Spatial overlap was determined by observation of flocks of coots and waterfowl. During ground counts (all years) and some aerial counts (1980), species composition of all waterbird flocks was recorded. Flocks were used as sample points to calculate coefficients of interspecific overlap (Ochiai 1957). We used Ochiai's coefficient

$$r_0 = \frac{A}{(A + B)(A + C)},$$

where A is the number of flocks containing both species, B is the number of flocks containing species one but not species two, and C is the number of flocks containing species two but not species one. Ochiai's coefficient was chosen because it satisfies the six necessary criteria for overlap indices (Janson 1981). The coefficient was calculated for each coot-duck species-pair for all duck species observed. Ochiai's coefficient ranges from zero (no overlap in use of space) to one (total overlap in use of space). To determine if spatial overlap changed through fall migration, we combined data for all years and calculated Ochiai's coefficient for September through December.

During ground counts, we observed mixed flocks of coots and waterfowl for at least 5 min to determine the principal behavioral interactions between coots and each duck species in flocks.

Because a similar diet between coots and a waterfowl species may partially explain behavioral interactions, we collected coots and three common species of ducks at sympatric feeding sites to determine overlap in diet. Gadwalls, wigeons, and coots were collected from all reservoirs. Redheads (*Aythya americana*) rarely fed at Robert S. Kerr Reservoir and therefore were collected only on Lake Carl Blackwell and Sooner Lake.

Birds were collected after they were observed feeding for ≥10 min. Esophageal contents were removed immediately and flushed into bottles containing 80% ethanol to prevent post-mortem digestion (Swanson and Bartonek 1970). Appropriate references (Pennak 1953, Fassett 1957, Martin and Barkley 1961, Steyermark 1963, Borror et al. 1976) were used to identify esophageal contents in the laboratory. Foods were oven dried to constant weight for 10–12 hours at 100°C and weighed to the nearest mg on a Mettler analytical balance. Food-habit data were expressed as percentage dry weight and percent frequency of occurrence.

The degree of diet overlap among species was computed as:

$$C_0 = \frac{2 \sum_{i}^{t} (X_i Y_i)}{X_i^2 + Y_i^2}$$

where t is the total number of food species and X_i and Y_i the proportions of the diet comprised of food species i for two avian species (Morisita 1959). Values vary from 0, for distinctly different samples, to 1, when diets are identical. As foods differed among lakes, diets of birds were compared only when collected from the same lake. Statistical analyses were performed using the Statistical Analysis System (SAS Institute, Inc. 1982).

RESULTS

Twenty-one species of ducks and geese were present on the lakes, but the single White-winged Scoter (*Melanitta fusca*) seen was excluded from the analysis. Numbers of geese, Wood Ducks (*Aix sponsa*), Ring-necked Ducks (*Aythya collaris*), Common Goldeneyes (*Bucephala clangula*), and Buffleheads (*B. albeola*) were not significantly correlated with numbers of coots. All of these species except Ring-necked Ducks occurred in small numbers relative to other waterfowl. Numbers of Mallards (*Anas platyrhynchos*), Hooded Mergansers (*Lophodytes cucullatus*), and Common Mergansers (*Mergus merganser*) were significantly negatively correlated with numbers of coots for at least one lake or one year (Table 1). Numbers of Northern Shovelers (*Anas clypeata*), Gadwalls, American Wigeons, and Redheads were positively correlated with numbers of coots. Finally, significant correlations, both positive and negative, with coot numbers were found with Green-winged Teal (*Anas crecca*), Northern Pintails (*A. acuta*), Blue-winged Teal (*A. discors*), Canvasbacks (*Aythya valisineria*), and Lesser Scaup (*A. affinis*) (Table 1).

A total of 1099 flocks of coots and waterfowl were observed during fall 1979–1981, with 14 species of ducks recorded in mixed flocks (Table 2). Gadwalls and American Wigeons were most frequently recorded in mixed flocks, followed by Mallards, Redheads, and Ring-necked Ducks. Spatial overlap between coots and waterfowl species was highest for American Wigeon and Gadwall. Spatial overlap between coots and Ring-necked Ducks and American Wigeons increased through November, but declined in December (Table 3). Mallards and Gadwalls increased their relative

TABLE 1

SPEARMAN CORRELATION COEFFICIENTS BETWEEN NUMBERS OF AMERICAN COOTS AND NUMBERS OF WATERFOWL DURING FALL MIGRATION IN NORTH-CENTRAL OKLAHOMA, 1979–1981 (ONLY SPECIES WITH SIGNIFICANT CORRELATIONS ARE PRESENTED)

	Lake and year						
	1979		1980			1981	
Species	Carl Blackwell	All	Carl Blackwell	Sooner	All	Carl Blackwell	All
Mallard	−0.69[c]	0.36[a]	−0.52[b]	−0.60[c]	−0.21	0.08	0.06
Blue-winged Teal	−0.27	0.18	−0.06	0.37[a]	0.11	0.03	0.30
Northern Shoveler	0.01	0.15	−0.27	0.18	0.25	0.42[a]	0.51[b]
Gadwall	−0.04	0.43[a]	0.04	0.21	0.43[b]	0.62[c]	0.63[c]
American Wigeon	0.06	0.28	0.16	0.28	0.46[b]	0.52[b]	0.58[c]
Canvasback	−0.19	0.37[a]	−0.34	−0.13	0.05	0.27	0.36[a]
Redhead	0.03	0.41[a]	0.00	0.24	0.30	0.38[a]	0.26
Lesser Scaup	−0.00	0.40[a]	−0.24	−0.20	−0.16	0.35	0.29
Hooded Merganser	−0.13	0.19	−0.18	−0.58[c]	−0.34[a]	−0.17	−0.21
Common Merganser	−0.44[a]	0.25	−0.41[a]	−0.24	−0.13		
Ruddy Duck	0.44[a]	0.39[a]	−0.53[a]	0.17	0.30	0.27	0.37[a]

[a] $0.01 < P < 0.05$.
[b] $0.001 < P < 0.01$.
[c] $P < 0.001$.

occurrence in mixed flocks through December. Nearly 75% of the waterfowl in 184 mixed flocks did not interact with coots (Table 4). Cooperative feeding (ducks feeding on matter churned up by coots and vice versa) occurred between coots and Mallards, Gadwalls, American Wigeons, Redheads, and Ring-necked Ducks. Wigeons and Gadwalls were the only species observed robbing food from coots. Aggressive interactions between coots and ducks occurred in <5% of all flocks.

Submerged aquatic vegetation was the most common food for all species on all lakes. Vegetation eaten by coots, Gadwalls, and wigeons on Robert S. Kerr Reservoir included Eurasian watermilfoil, filamentous algae (*Cladophora* sp.), and floating-leaved pondweed (*Potamogeton nodosus*). Coots also grazed on sedges (*Cyperus* sp.), rushes (*Juncus* sp.), and cattail. A large number of snails was found in one coot. Aquatic insect larvae and adults were frequently eaten by coots, but amounts by dry weight were low.

On Sooner Lake, naiads were the principal food of coots, Gadwalls, and wigeons. Redheads also ate naiads, but sago pondweed (*Potamogeton pectinatus*) was found in most birds. One coot and one Gadwall contained only muskgrass (*Chara vulgaris*). Coots and Redheads ate small amounts of pondweed seeds. Naiads were also the most common food of coots,

TABLE 2

COEFFICIENTS FOR INTERSPECIFIC OVERLAP BETWEEN AMERICAN COOTS AND COMMON WATERFOWL SPECIES IN NORTH-CENTRAL OKLAHOMA, FALL 1979–81[a]

Species	Index of interspecific overlap[b,c]	Number of flocks with coots	Total number of flocks
Mallard	0.10 ± 0.01 D	43	367
Blue-winged Teal	0.02 ± 0.02 B	3	42
Northern Shoveler	0.02 ± 0.03 B	2	15
Gadwall	0.20 ± 0.04 F	70	262
American Wigeon	0.20 ± 0.04 F	68	239
Canvasback	0	0	25
Redhead	0.12 ± 0.04 E	30	141
Lesser Scaup	0.02 ± 0.02 B	3	54
Hooded Merganser	0.03 ± 0.20 C	3	24
Common Merganser	0	0	19
Ruddy Duck	0.01 ± 0.02 A	1	28

[a] Number of flocks = 1099; number of flocks with coots = 483.
[b] Ochiai's coefficient of interspecific overlap ± 95% confidence interval.
[c] Means having the same letter are not significantly different (t-test, $P = 0.01$).

Redheads, Gadwalls, and wigeons on Lake Carl Blackwell, where muskgrass was the only food found in one coot and one wigeon.

Coots and ducks fed on many of the same foods during fall. Coots, Gadwalls, and wigeons ate similar foods within all lakes (Table 5). Redheads and coots ate similar foods on Lake Carl Blackwell, but Redheads were the only species eating narrow-leafed pondweed on Sooner Lake, accounting for the low diet overlap with coots.

DISCUSSION

Chronology of migration of most coots and ducks in our study differs both seasonally and daily. Negative correlations among the migration chronology of coots and other species were related to early migration of Blue-winged Teal or to late migration of Mallards and Common Mergansers relative to coot migration. For those species with migration positively correlated with migration of coots, such as Gadwall, American Wigeon, and Northern Shoveler, differences between migration timing of coots and individual species of ducks were explained by differences between responses of migrating coots and ducks to the passage of cold fronts. Waterfowl characteristically arrive ahead of or just behind fronts and frequently migrate during the day (Richardson 1978). Coots, however, follow cold fronts and are night migrants (Ryder 1963). Therefore, peak numbers of coots often followed peak numbers of waterfowl by one day. Because most coots and ducks usually left our study lakes within one to

TABLE 3

CHANGES IN SPATIAL OVERLAP BETWEEN AMERICAN COOTS AND COMMON WATERFOWL SPECIES THROUGH FALL MIGRATION, SEPTEMBER–DECEMBER 1979–81

	September		October		November		December	
	Index[a] of overlap	n_1/n_2[b]	Index of overlap	n_1/n_2	Index of overlap	n_1/n_2	Index of overlap	n_1/n_2
Mallard	0.05 (A)	1/5	0.07 (A)	14/112	0.17 (B)	16/139	0.23 (C)	12/111
Gadwall	0.08 (A)	2/9	0.21 (B)	50/178	0.22 (B, C)	14/63	0.23 (C)	4/12
American Wigeon	0.14 (A)	5/20	0.18 (B)	42/170	0.33 (C)	16/37	0.29 (D)	5/12
Redhead	0	0/1	0.12 (A)	23/109	0.16 (B)	7/31		
Ring-necked Duck	0	0/1	0.06 (A)	8/59	0.13 (B)	5/23	0.08 (C)	1/6

[a] Ochiai's index for interspecific overlap using flocks as sample points, indices having the same letter are not significantly different (t-test, $P = 0.01$).
[b] Number of flocks containing coots (n_1)/number of flocks containing waterfowl species (n_2).

TABLE 4

BEHAVIORAL INTERACTIONS BETWEEN WATERFOWL AND AMERICAN COOTS IN 184 MIXED FLOCKS, FALL 1979–81

Species	Behavioral interaction					
	None	Aggression toward coots	Aggression toward ducks	Cooperative feeding	Food robbery	Total no. of flocks observed containing species
Mallard	19 (90.5)[a]	0	0	2 (9.5)	0	21
Northern Pintail	6 (85.7)	0	1 (14.3)	0	0	7
Blue-winged Teal	3 (75.0)	0	1 (25.0)	0	0	4
Gadwall	33 (70.2)	1 (2.1)	1 (2.1)	7 (14.9)	5 (10.6)	47
American Wigeon	36 (70.6)	1 (2.0)	1 (2.0)	8 (15.7)	5 (9.8)	51
Redhead	19 (67.9)	0	0	9 (32.1)	0	28
Ring-necked Duck	8 (66.7)	0	0	4 (33.3)	0	12
All species	137 (74.5)	2 (1.1)	5 (2.7)	30 (16.3)	10 (5.4)	184

[a] Number of interactions in each category (% of total for the species).

two days (Eddleman et al. 1985), potential temporal overlap of coots and waterfowl was minimized.

Spatial overlap for all coot-waterfowl pairs increased as the season progressed. This increase may indicate a proportional decrease of all aquatic food plants. As waterfowl deplete food in shallow water, the activities of coots make food available in deeper water as a result of churning, thus permitting food robbery by ducks. Coots fed on matter churned up by ducks only once. Food robbery was initiated by American Wigeon and Gadwall, two species that usually do not dive in deep water and which consume foods similar to those eaten by coots (Knapton and Knudsen 1978, Paulus 1982). Cooperative feeding and food robbery allowed dabbling ducks to obtain food that was ordinarily unavailable to them (Knapton and Knudsen 1978, Ryan 1981). Cooperative feeding may also benefit coots (Ryder 1959, Anderson 1974). We found no evidence that coots robbed food from ducks, although this behavior has been observed in coots and Ring-necked Ducks on wintering areas (L. D. Vangilder, pers. comm.).

We noted few instances of aggression between coots and ducks during fall migration. Interspecific behavioral interactions between breeding coots and ducks peak after hatching of coot broods (Ryder 1959, Ryan and Dinsmore 1979). At that time coots tenaciously defend broods against any species of duck entering their territory.

Overlap in diet among coots and the four principal waterfowl species was high on certain lakes in our study, especially between coots and

TABLE 5

DIET OVERLAP VALUES (MORISITA 1959) BETWEEN AMERICAN COOTS AND GADWALLS, AMERICAN WIGEONS, AND REDHEADS ON ROBERT S. KERR RESERVOIR, SOONER LAKE, AND LAKE CARL BLACKWELL DURING FALL 1980

	Gadwalls	American Wigeons	Redheads
Robert S. Kerr Reservoir	0.80	0.75	
Sooner Lake	0.99	0.99	0.24
Lake Carl Blackwell	0.86	0.90	0.86

Gadwall and American Wigeon. This overlap may explain the high incidences of behavioral interactions between coots and these two species compared with other ducks. Redheads differed from coots in eating mostly sago pondweed on Sooner Lake. Overall diets were similar in that vascular aquatic vegetation predominated in the diets of both species.

Interactions between coots and waterfowl on nesting areas usually benefit waterfowl or have little effect on densities of waterfowl (Ryder 1959, Knapton and Knudsen 1978, Nudds 1981). Similar conclusions are apparent during migration, although food robbery by ducks and churning up of food material by coots provide foods otherwise unavailable to some dabbling ducks.

SUMMARY

Temporal, spatial, and behavioral relationships between migrating American Coots (*Fulica americana*) and ducks were investigated in fall 1979–1981 in Oklahoma. Diets of coots, Gadwalls (*Anas strepera*), American Wigeons (*A. americana*), and Redheads (*Aythya americana*) were studied in fall 1980. Arrivals and departures of coots differed from those of waterfowl for all species, mainly because waterfowl migrated ahead of cold fronts and often diurnally, while coots migrated behind cold fronts and nocturnally. Significant positive correlations occurred between numbers of coots and numbers of Northern Shovelers (*Anas clypeata*), Gadwalls, American Wigeons, and Redheads on at least some lakes in most years. Waterfowl occurred in mixed flocks with low frequency. Gadwalls and American Wigeons were most frequently recorded with coots. Most ducks did not interact with coots in mixed flocks. Cooperative feeding and food robbery were the most frequently recorded behavioral interactions, especially between coots and Gadwalls or American Wigeons. Foods of coots and ducks were similar in most lakes and consisted mostly of aquatic vegetation. Interspecific interactions between coots and ducks are minimal because of temporal and spatial segregation during migration, and behavioral interactions that are mostly neutral or beneficial to ducks.

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WETLAND SELECTION BY MALLARDS AND BLUE-WINGED TEAL

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A precursor to the question of which environmental and physiological factors influence habitat choice is the question of whether organisms *select* (defined here as exhibiting a preference) habitat at all, and if so, what constitutes evidence of habitat preference. Hildén (1965) suggested that birds choose the best available habitat. It does not follow, however, that the observed distributions of organisms are the result of habitat preference, because birds may be constrained in their choice of habitat by geophysical events and the effects of interactions within and among species (Partridge 1978).

Habitat use by breeding ducks often has been studied (e.g., Evans et al. 1952, Evans and Black 1956, Bengston 1971, Smith 1971, Stoudt 1971, Dwyer et al. 1979, Wheeler and March 1979) with the implicit or explicit purpose of delineating "critical habitats." Biologists have attempted to determine habitat preferences of ducks by correlating duck densities with environmental variables (e.g., Lokemoen 1973, Stewart and Kantrud 1974, Weller 1979, Joyner 1980, Godin and Joyner 1981). From these types of analyses, it is usually concluded that the "preferred" habitats are those with an abundance of the habitat features correlated with duck density.

Here, we present results of a multivariate analysis of selection of structurally different wetlands by breeding Mallards (*Anas platyrhynchos*) and Blue-winged Teal (*A. discors*). Our objectives were (1) to test whether Mallards and Blue-winged Teal exhibit habitat selection as evidenced by disproportionate use of habitats, (2) to examine whether there is interspecies variation in the tendency for each species to select habitats, and (3) to test whether breadth of habitat use is related to density of birds.

STUDY AREA AND METHODS

The study was conducted from late April to mid-August, 1977 to 1980, on 388.5 ha of aspen parkland approximately 47 km east of Saskatoon, Saskatchewan. Complete descriptions of the area can be found in Sugden (1977). Ninety-eight wetland basins were present on the study area, but the number with standing water varied annually and seasonally.

Duck censuses.—Five censuses were conducted at 10-day intervals from late April to mid-June each year, except in 1979 when a late spring delayed surveys for approximately 10 days.

Counts were conducted on all ponds by walking through the area, except where wetlands were close to roads and observable from a vehicle. All Mallard and Blue-winged Teal pairs, lone drakes, lone hens, and groups of drakes were recorded. Total males and females were

noted and discernible pairs within flocks of the same species were recorded. All counts were conducted between 08:00 and 12:00 h when pairs and drakes were least mobile (Diem and Lu 1960, Dzubin 1969). Censuses were not made during periods of rain or high winds, but they were continued during periods of cloud cover. An effort was made not to disturb the ducks during counts so as to minimize the risk of counting them twice. Two investigators worked together, enabling one to determine the destination of birds that flushed and to adjust counts accordingly.

Brood surveys were conducted, at approximately 15-day intervals, from late June to mid-August. Either five (1977) or four (1978–80) surveys were conducted annually during early morning and late evening when broods were feeding and most visible (Ringelman and Flake 1980). All observations were used in the analyses of habitat selection.

Brood production on the study area was estimated initially using the method developed by Gollop and Marshall (1954). This estimate was modified by including broods whose age class indicated they were present on previous surveys, but not seen and recorded. We then assumed that breeding pair density was related to brood production. To determine which of the birds present on the study area during the breeding period could be designated members of breeding pairs, the brood production of each species was regressed against four different breeding pair densities: total ducks, observed pairs, observed pairs plus single males, and observed pairs plus males in groups of five or less. The index that accounted for the most variation in the number of broods was selected as the best estimate of breeding pairs, and all observations of adult birds so designated were used in analyses of habitat selection.

Habitat measurements.—Pond size and several features of emergent and upland vegetation immediately surrounding the ponds were recorded during each census. The percentage of the pond surface covered by emergent vegetation was assigned to one of five categories (0–10%, 11–25%, 26–50%, 51–75%, and >75%). Vegetation height was assigned to one of five classes (0–0.25 m, open water and low mat vegetation; 0.25–0.50 m, wet meadow vegetation; 0.5–1.0 m, sedge [*Carex* sp.] and white-top grass [*Scholochloa festuacaea*]; 1.0–2.0 m, cattail [*Typha latifolia*]; and 2.0 m, shrubs and trees). Interspersion of emergent vegetation and water was assigned to one of three classes: uniform, partially interspersed, or heavily interspersed (after Stewart and Kantrud 1971). Trees and shrubs were coded as not present, partially surrounding, or completely surrounding the ponds. The structure of vegetation was coded by classes of vegetation stature: low (summer-fallow fields), intermediate (native grasses), and tall (cereal crops).

Statistical methods.—To distinguish between proportionate (non-selective) and disproportionate (selective) use of available wetlands, we constructed three models of habitat use in relation to habitat availability (Fig. 1). If there was no statistical difference between the structural distributions of wetlands available and the structural distributions of wetlands used by ducks (Model A) (Fig. 1), we rejected the hypothesis that the ducks selected wetlands (i.e., habitat use simply "mapped" to habitat availability). When the ponds used by ducks differed from those available, however, it may have been due either to changing such habitat preferences relative to varying habitat availability (Model B) (Fig. 1), or to stenotopic habitat use despite varying habitat availability (Model C) (Fig. 1). In drought years, for example, only deep, large, permanent ponds are generally available; in other years, a wide assortment of ponds, both shallow and small, and deep and large, is available. To test among these alternatives, we used data on habitat use by Mallard and Blue-winged Teal breeding pairs and hens with broods in two structural habitat dimensions constructed from principal components analysis (PCA; Nie et al. 1970).

Data analysis.—Three sets of principal component (PC) scores were used to characterize wetland habitat. Two of these sets described the structure of all wetlands in the study area during breeding and brood-rearing. These are referred to as the "May ponds" (all wetland

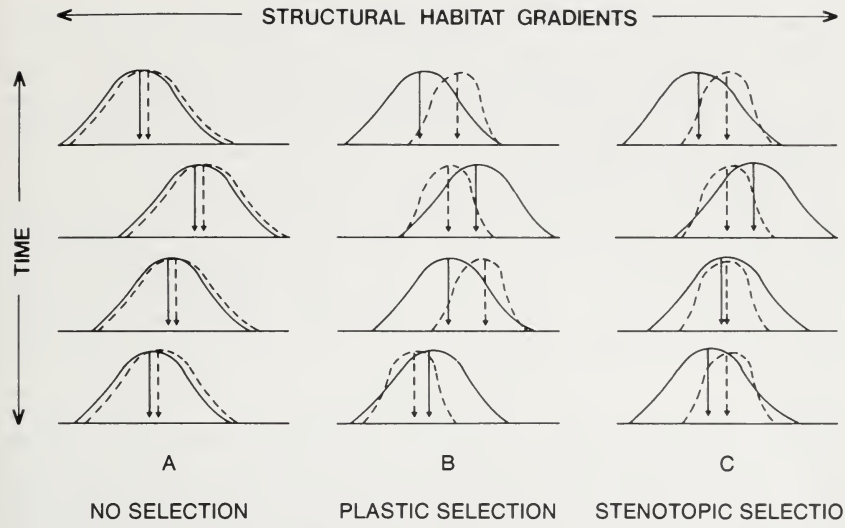

FIG. 1. Three models of habitat use (— — —) in relation to habitat availability (——) representing variation over four time units. In each model, temporal variation in habitat availability is the same, but difference in habitat use patterns can result in three types of habitat "selection." A = No selection: habitats used "map to" those available. B = "Plastic" habitat selection: habitats used are statistically different from those available but not temporally consistent. C = "Stenotopic" habitat selection: habitats used are statistically different from those available and consistent through time, despite variation in available habitats.

basins containing water on the first census of breeding pairs) and the "July ponds" (all basins containing water during the first brood census after shallow, ephemeral wetlands dried up). The third set of principal component scores described the structure of all wetlands used by ducks during breeding and brood-rearing (i.e., subsets of "May ponds" and "July ponds"). These are referred to as "Duck ponds." The component scores of wetlands used by pairs were compared with the component scores of the wetlands available during May; the component scores of the wetlands used by broods were compared with the component scores of those available in July.

Between-year variation in wetland availability due to the annual variability in wetness regimes presented a problem when attempts were made to distinguish among the alternative types of habitat use displayed in Fig. 1. In particular, due to the presence and absence of different structural types of wetlands in "wet" and "dry" years, different habitat variables might have contributed differentially to the construction of the principal components from year to year. We pooled data across years within each data set to make the resultant principal component scores all relative to long-term average habitat conditions, thereby facilitating comparison of PC scores among years on a common scale (Nudds 1983).

The variable loadings on the first principal component for May ponds were compared with the loadings on the first principal component for Duck ponds, loadings on the second principal component for May ponds were compared with loadings on the second principal component for Duck ponds, etc. (Rotenberry and Wiens 1980:1242–1243, Landres and MacMahon 1983:186) with Spearman ranked order correlation. Nonparametric correlations

were used because the distribution of variable loadings was unknown and because degrees of freedom was small (N = 6 variable loadings). If the correlations were significant, we declared the axes derived from each principal component analysis sufficiently similar to warrant direct comparison of the distributions of scores on those axes. If the ranked order correlations were insignificant, we declared the habitats used different from those available (i.e., selection occurred) and that inspection of the variable loadings would yield information about how the wetlands used differed from those available.

If the ranked order correlations were significant, we compared variation in principal component scores between wetlands used and wetlands available in two ways to determine if the wetlands used by pairs and hens with broods of either species differed in any year from those available (Model A vs Model B or C) (Fig. 1). First, Student's *t*-tests were used to test for differences in mean location of birds in structural habitat space with the mean location of habitats available in that space. Second, we compared the variance in structural habitats used by birds with the variance in the habitats available. Significant differences in the mean of characteristics of those wetlands used vs those available, or significantly narrower variance in wetlands used vs those available, were considered evidence of habitat selection.

We were liberal at setting rejection levels for the null hypothesis of no habitat selection because comparing a distribution that is a subset of another tends to increase the chance of committing a Type II error. On the other hand, the replication of observations on the same breeding pairs of each species implies a lack of independence among observations which would tend to increase the chance of committing a Type I error. We chose $\alpha = 0.10$ in analyses of both pairs and broods as a compromise rejection level.

If birds were found to be selecting habitats, we used ANOVA to compare the magnitude of the among-year variation in the structure of used and available wetlands, thereby distinguishing between stenotopic and plastic selection (Model B vs Model C) (Fig. 1). If among-year variation in wetlands used was greater than among-year variation in wetlands available, then habitat selection was plastic (Model B). If, however, the distributions of wetlands used varied less through time than did the distribution of wetlands available, then habitat selection was relatively consistent even though habitat available changed from year to year (Model C).

RESULTS

Breeding pair abundance.—Observed pairs plus males in groups of five or less accounted for the most variance in brood abundance for both Mallards and Blue-winged Teal (Table 1). For Mallards, this index was significant ($P < 0.05$), but for Blue-winged Teal it was not. Therefore, the total of observed pairs plus males in groups of five or less was also used as the best estimate of Blue-winged Teal breeding pairs. This finding is consistent with those of other studies; Hammond (1969), Wheeler and March (1979), and Ruwaldt et al. (1979) used this index of breeding pairs for dabbling ducks. Hereafter, breeding pairs, or simply pairs, refers to observed pairs plus males in groups of five or less. All individuals so recorded comprised the sample of ducks on which the determination of wetland use by breeding pairs was based. Sample sizes for analyses of habitat selection by pairs and hens with broods are given in Table 2.

Comparison of principal component loadings for different data sets.—In all data sets, wetlands were arrayed along the first principal axis from open ponds with low vegetation to closed ponds with tall emergent vege-

TABLE 1

REGRESSION STATISTICS (SLOPE AND *t*-TEST OF ITS DIFFERENCE FROM ZERO) OF VARIOUS INDICES OF BREEDING PAIR ABUNDANCE AND BROOD ABUNDANCE

Indices of pair abundance	Mallard		Blue-winged Teal	
	Slope	t_{18}	Slope	t_{18}
Total ducks	0.45	2.19[a]	0.20	0.89
Observed pairs	0.08	0.38	0.19	0.83
Observed pairs plus single males	0.09	−0.39	0.26	1.15
Observed pairs and groups of five males or less	0.46	2.25[a]	0.28	1.26

[a] $P < 0.05$.

tation. The second principal axis denoted a gradient of increasing pond size and vegetation interspersion (Table 3). The structures of the same principal components from each data set were similar (Table 4).

Habitat use by ducks.—There were no differences between the distributions of wetlands used by Mallard pairs and the distributions of wetlands available in May ($P > 0.10$) (Table 5). Neither did Mallard pairs use a narrower range of wetlands than those available. Thus, we could not detect wetland selection by Mallard pairs, and they appeared to use structurally different wetlands in proportion to their availability.

Three of eight *t*-tests between component scores of May wetlands and those wetlands used by pairs of Blue-winged Teal were significant ($P < 0.05$) (Table 5). In 1977, on PC1, pairs of Blue-winged Teal chose closed ponds characterized by tall vegetation. In 1978, on PC2, pairs of Blue-winged Teal selected large ponds interspersed with emergent vegetation, but in 1979, on PC2, they selected small ponds with uniform vegetation. In addition, pairs of Blue-winged Teal used a narrower range of wetlands than was available on PC1 in 1978.

Mallard broods showed some evidence of habitat preference but, in general, used wetlands in proportion to their availability. The only differences between wetlands used by Mallard broods and the wetlands available in July were in 1977 and 1979 (Table 6) when Mallard broods, on PC2, selected large wetlands interspersed with vegetation. These were the two years when there were few Mallard broods (Table 2). In 1978, Mallard broods used a narrower range of wetlands than was available on PC1.

Four of eight *t*-tests between component scores of July wetlands and component scores of wetlands used by broods of Blue-winged Teal were significant (Table 6). In 1979 and 1980, on PC1, they selected open ponds characterized by low vegetation. In 1977 and 1978, they used a narrower range of wetlands than was available on PC1. In 1977 and 1978, on PC2,

TABLE 2
SAMPLE SIZES USED IN THE ANALYSES OF HABITAT SELECTION BY MALLARD AND BLUE-WINGED TEAL PAIRS AND HENS WITH BROODS

Year	Number of wetlands		Breeding pairs[a]		Broods	
	May	July	Mallard	Teal	Mallard	Teal
1977	66	46	228	238	6	35
1978	82	33	219	124	15	21
1979	98	66	129	98	8	21
1980	90	40	282	136	21	26
Total	336	185	868	596	50	103

[a] Breeding pairs include observed pairs and males in groups of five or less. Figures are totals of five censuses in each year. Because broods are relatively sedentary, although pairs move from wetland to wetland, brood abundance is an estimate of the minimum number of broods present; breeding pairs is the total number of observations of pairs.

broods of Blue-winged Teal chose large ponds interspersed with emergent vegetation. These same trends were evident in 1979 and 1980, but were not significant; however, in 1979 teal used a significantly narrower range of wetlands than was available on PC2. These patterns bore no relationship to density of broods of Blue-winged Teal (Table 2).

Pairs and broods of Mallards generally exhibited Model A (Fig. 1) habitat use. Blue-winged Teal pairs, however, varied more in their selection of wetlands than did wetland availability in either habitat dimension (Table 7); thus they followed Model B (Fig. 1) habitat selection. Conversely, teal broods were relatively stenotopic in their selection of wetlands (Model C) (Fig. 1) in the first habitat dimension, but plastic (Model B) in their selection of wetlands in the second habitat dimension (Table 7).

DISCUSSION

Pairs of breeding Mallards were not selective but generally used structurally different wetlands in proportion to their availability. Other studies have reported a similar lack of preference for breeding habitat by Mallards. For example, Dwyer et al. (1979) studied the use of prairie potholes by Mallards in south-central North Dakota and concluded that there were no preferences in the use of different wetlands. Patterson (1976) studied Mallard use of heterogeneous beaver ponds in Ontario and found that pairs were evenly distributed over all ponds. In contrast, Gilmer et al. (1975) studied habitat use by Mallards in the forested region of north-central Minnesota and found that they preferred seasonal wetlands, sand-bar ponds, and overhanging brush shorelines, although they recognized this species was ubiquitous and capable of utilizing a wide variety of habitats.

Pairs of Blue-winged Teal used wetlands disproportionately in three of

TABLE 3
FACTOR LOADINGS AND AMOUNT OF VARIANCE ACCOUNTED FOR BY PCA RUN ON MAY PONDS, JULY PONDS, AND DUCK PONDS

Variables	May ponds		July ponds		Duck ponds	
	PC1	PC2	PC1	PC2	PC1	PC2
Pond size	−0.13	0.82	−0.29	0.80	−0.31	0.83
Vegetative cover	0.75	−0.32	0.83	−0.06	0.76	−0.12
Vegetation height	0.80	−0.05	0.68	0.29	0.58	0.33
Interspersion of vegetation	0.09	0.68	0.12	0.77	0.18	0.79
Structure of peripheral vegetation	0.57	0.36	0.50	−0.01	0.68	0.05
Upland vegetation	0.39	0.10	0.14	0.00	0.45	−0.04
Cumulative variance accounted for	53.3%		48.1%		53.5%	

four years, but the structure of wetlands they chose varied annually. Reasons for this inconsistency in habitat selection are not apparent; teal might have cued on some habitat features not measured and uncorrelated with any of the features included in these analyses. Pond fertility, available food resources, water depth, and amount of submergent vegetation were not measured and may have been important to birds in the selection of wetlands (Ringelman and Longcore 1982, Talent et al. 1982). Structural habitat features, such as we measured, however, appear to act as proximate cues to food-rich areas (e.g., Kaminski and Prince 1981, Murkin et al. 1982) so it is not clear whether the omission of data on submerged vegetation and food density would substantially alter our conclusions. Habitat selection by Blue-winged Teal has been demonstrated elsewhere. Stewart and Kantrud (1973) found a disproportionate number of pairs of Blue-winged Teal on shallow seasonal wetlands in the prairie pothole region of North Dakota. Fifty-two percent of all Blue-winged Teal were found on seasonal wetlands, yet seasonal wetlands represented only 21% of the available habitat. In a second study, Steward and Kantrud (1974) found yearly variations in abundance of Blue-winged Teal were correlated with the abundance of seasonal wetlands. Evans and Black (1956) reported that pairs of Blue-winged Teal preferred large wetlands early in the breeding season. Dispersion to smaller wetlands did not occur until May when numbers of pairs increased and larger wetlands appeared crowded. Blue-winged Teal showed a preference for larger wetlands at our study site in 1978. Perhaps there were sufficient large wetlands to accommodate Blue-winged Teal in 1978 and dispersion to smaller wetlands did not occur.

TABLE 4

SPEARMAN RANK CORRELATION (N = 6 VARIABLES) BETWEEN VARIABLE LOADINGS ON PRINCIPAL COMPONENTS DESCRIBING DUCK PONDS WITH EACH OF MAY PONDS AND JULY PONDS

Component scores correlated	Principal component 1		Principal component 2	
	r_s	P	r_s	P
Wetlands used by pairs with wetlands available in May	0.82	0.021	0.82	0.021
Wetlands used by broods with wetlands available in July	0.94	0.002	0.94	0.002

With the exception of 1977 and 1979, when Mallard broods chose large wetlands interspersed with vegetation, and 1978, when they selected wetlands with intermediate vegetative cover, Mallards used wetlands in proportion to their availability. In contrast, Evans et al. (1952) found that Mallard broods used small potholes but were still the most widely distributed species. As in our study, Bengston (1971) and Courcelles and Bédard (1979) found that Mallard broods used ponds containing emergent vegetation. This may have been related to the availability of invertebrates (Talent et al. 1982), which are more common in vegetated ponds than those lacking vegetation (Krull 1970), and are important foods of duck-

TABLE 5

RESULTS OF *t*-TESTS AND *F*-TESTS ON PRINCIPAL COMPONENT SCORES OF MAY PONDS USED BY MALLARD AND BLUE-WINGED TEAL PAIRS

Year	May ponds		Mallard				Blue-winged Teal			
	$\bar{x}$	s^2	$\bar{x}$	s^2	$P^{t a}$	$P^{F b}$	$\bar{x}$	s^2	P^{t}	P^{F}
PC1										
1977	−0.11	0.81	0.07	0.82	NS	NS	0.31	0.83	0.001	NS
1978	−0.12	1.14	−0.20	0.87	NS	NS	−0.30	0.66	NS	0.007
1979	0.03	1.10	0.11	0.90	NS	NS	−0.03	1.15	NS	NS
1980	0.16	0.89	0.01	1.43	NS	NS	0.18	1.19	NS	NS
PC2										
1977	0.39	1.07	0.21	1.16	NS	NS	0.15	1.09	NS	NS
1978	−0.10	0.86	−0.16	0.78	NS	NS	0.45	1.11	0.001	NS
1979	−0.96	1.03	−0.24	0.82	NS	NS	−0.37	0.76	0.045	NS
1980	−0.09	0.95	−0.23	0.81	NS	NS	−0.26	1.03	NS	NS

[a] P^{t} is the probability of a two-tailed pairwise *t*-test adjusted, if necessary, for unequal variances.
[b] P^{F} is the probability of a one-tailed *F*-test for equality of variances.

TABLE 6

RESULTS OF *t*-TESTS AND *F*-TESTS ON COMPONENT SCORES OF JULY PONDS USED BY MALLARD AND BLUE-WINGED TEAL BROODS

	July ponds		Mallard				Blue-winged Teal			
Year	$\bar{x}$	s^2	$\bar{x}$	s^2	P^a	P^{Fb}	$\bar{x}$	s^2	P^a	P^F
PC1										
1977	−0.45	0.91	−0.11	0.66	NS	NS	−0.20	0.22	NS	0.001
1978	−0.15	1.30	0.25	0.27	NS	0.003	−0.43	0.59	NS	0.001
1979	0.29	0.73	−0.06	1.05	NS	NS	−0.22	0.44	0.01	NS
1980	0.16	0.93	−0.27	2.14	NS	NS	−0.43	0.55	0.01	NS
PC2										
1977	0.15	1.03	1.20	0.49	0.01	NS	0.78	0.88	0.01	NS
1978	−0.00	0.96	0.23	0.49	NS	NS	0.68	1.03	0.01	NS
1979	−0.15	1.00	0.54	0.78	0.06	NS	0.02	0.23	NS	0.001
1980	0.08	0.99	−0.03	0.41	NS	NS	0.29	0.72	NS	NS

[a] P^a is the probability of a two-tailed pairwise *t*-test adjusted. if necessary, for unequal variances.
[b] P^F is the probability of a one-tailed *F*-test for equality of variances.

lings (Chura 1961, Collias and Collias 1963, Perret 1962, Sugden 1973, Driver et al. 1974).

Broods of Blue-winged Teal showed stenotopic selection for open wetlands characterized by little vegetation. Stoudt (1971), Lokemoen (1973), and Mack and Flake (1980) also found that broods of Blue-winged Teal used open wetlands and relied on open water and diving for escape. Evans et al. (1952) and Courcelles and Bédard (1979), however, found that teal broods were associated with emergent vegetation. In 1977 and 1978, we also found that broods of Blue-winged Teal disproportionately used large wetlands with interspersed vegetation, but they were more plastic in their

TABLE 7

ANOVA TESTS FOR VARIABILITY IN HABITAT USE BY BLUE-WINGED TEAL PAIRS AND BROODS VERSUS VARIABILITY IN HABITAT AVAILABILITY IN MAY AND JULY

Period	Habitat dimension	*F*	*P*	Population component	*F*	*P*
May	PC1	1.5	0.22	Pairs	11.8	0.0001
	PC2	4.2	0.006	Pairs	17.2	0.0001
July	PC1	6.2	0.0005	Broods	1.13	0.34
	PC2	1.04	0.38	Broods	4.19	0.008

selection of wetlands in that habitat dimension than in the other (see also Weller 1979).

One prominent hypothesis about habitat selection is that only the best habitats are used when the number of animals in a population is low (Hildén 1965, Fretwell and Lucas 1969, Partridge 1978). The pattern of selection in the first habitat dimension by Blue-winged Teal hens with broods in 1979 seems to support the hypothesis, because one would expect habitat preferences to be most evident in 1979 when a large number of ponds was available for the lower than average number of broods (Table 2); however, selection was evident in at least one dimension in all of the other years as well (Table 6). The pattern of selection by Mallard broods may also be consistent with the hypothesis. Selection was evident in 1977 and 1979 (Table 6), i.e., in those years when wetland numbers were high and brood density was low (Table 2). Similarly, Talent et al. (1982) found evidence of disproportionate use of some wetlands by Mallard broods when wetlands were abundant, but habitat use conformed to habitat availability when wetlands were more scarce.

We conclude that both Mallards and teal select wetlands, particularly during brood-rearing, but that wetland use most often conforms to wetland availability. The dynamic nature of wetland habitats, and the corresponding spatial and temporal variation in the requisites for successful breeding by waterfowl, appear to have selected for plastic habitat-use strategies by ducks. Consequently, different components of entire wetland complexes might all be important at different times during the breeding period (Patterson 1976, Swanson et al. 1979, Duebbert and Frank 1984).

SUMMARY

Four years of observations of habitat use by breeding pairs and broods of Mallards (*Anas platyrhynchos*) and Blue-winged Teal (*A. discors*) were used to test the hypothesis that prairie-nesting ducks exhibit wetland preferences (i.e., select habitat). Mallard pairs did not select wetlands. Mallard broods selected large wetlands with interspersed vegetation when brood density was low. Pairs of Blue-winged Teal selected wetlands, but were inconsistent in their choices. Broods of Blue-winged Teal consistently selected open wetlands with vegetation of low stature, but patterns of wetland selection by broods of Blue-winged Teal bore no consistent relationship to brood density.

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TIME-ACTIVITY BUDGET FOR BREEDING GREATER GOLDEN-PLOVERS IN NORWEGIAN MOUNTAINS

INGVAR BYRKJEDAL

Precocial birds, including shorebirds, are more predisposed toward the evolution of uniparental egg and brood care than are altricial birds, as their chicks usually feed themselves (e.g., Wittenberger and Tilson 1980). In extreme cases, as in polygynous and polyandrous systems, incubation and brood-care may be left entirely to one mate; in species with a "rapid multiclutch system" (Hildén 1975, 1979) the mates care for one brood each. In many monogamous species the brood is sooner or later left in care of one of the parents, often the male (Pitelka et al. 1974).

In the Greater Golden-Plover (*Pluvialis apricaria*) both parents take part in the breeding duties (Nethersole-Thompson and Nethersole-Thompson 1961, Byrkjedal 1978a, Parr 1980), although males may be solely in charge of broods late in the season (Byrkjedal 1978a). Apparently, in the Greater Golden-Plover, cooperation by both mates through most of the season is needed for successfully rearing young. Based on a time-activity study of Greater Golden-Plovers in southern Norway, I analyze the labor division between males and females and discuss why a biparental mating system is maintained.

MATERIAL AND METHODS

Sampling of data.—The data were collected from a Greater Golden-Plover population at 1200–1300 m elevation in the middle alpine zone at Hardangervidda, southern Norway, in the summers of 1979–1981. The study area is described by Byrkjedal (1978a) and Kålås and Byrkjedal (1984a).

The time-activity budget is based on "focal-animal sampling" (Altmann 1974) applied to visual observations and radio-tagged birds. Visual observations were done on six pairs in the prelaying period, two pairs on nest, four off-duty females during the incubation period, and three pairs with chicks between 1 and 11 days old. Radio-tagging was attempted using transmitters (TX142-1S, weighing 3–4 g) emitting a pulsing "beep" signal detectable up to about 1000 m. Transmitters were glued to the back feathers of birds. As transmitters came off with molt, useful data were obtained only from one male in the incubation period and one female after hatching. In addition to the two nests observed visually, nest attendance was monitored in five nests with a Grant thermograph connected by a sub-surface wire to a thermistor pointing up amidst the eggs. The thermograph recorded nest temperatures continually for 3–6 days. The sex of the incubating bird was identified on 58 nest inspections at 16 nests.

Activities recorded visually were alert and non-alert feeding (defined by alert and non-alert stances between pecks) (Fig. 1), standing and running alertly, agonistic behavior (inter- and intraspecific aggressiveness), courtship, running and flying (while not being alert, or

chasing other birds, or feeding), preening, standing inactively (relaxed posture) (Fig. 1), and sleeping. "Alert feeding" took place only in the posthatching period, and in the construction of the time budget half the "alert feeding" time was assigned to "alertness" and half to "feeding." For birds sitting on the nest, I also recorded tossing of nest material into the nest, alertness, freezing, and on and off periods. As assessed through several hours of simultaneously viewing the birds and listening to the radio signal, the radio-tagging allowed me to distinguish (1) flight, (2) running on the ground or preening, (3) staying motionless, or (4) feeding. The frequency of aerial display through the 1981 season was noted during some of the visual observation sessions by recording for each minute whether aerial display (from any bird, not just the one under observation) had occurred.

Finally, feeding methods and pecking rates were recorded, both during time-activity observations, and in separate observation sessions. I distinguished (1) pecking at vegetation (indicated feeding on berries and adult insects [Byrkjedal 1980]), (2) pecking at the ground (indicated feeding on adult insects, especially carabids), and (3) probing in the ground (indicated feeding on larvae and earthworms). Birds were observed for at least 20 min while feeding. Altogether 2372 pecks were classified during a total of 777 min of observations on actively feeding birds. Body condition index (100 × weight [g]/wing length [mm]) was obtained from birds shot for stomach analyses in 1974 and 1975 (Byrkjedal 1980) and from birds trapped for banding.

The observed birds were individually recognizable by color bands or characteristic plumage markings, except the four off-duty females. The behavior of these females was studied at the edge of a large bog, where there were no golden-plover territories. A varying number of golden-plovers stayed there during the season, most of them having female-like plumage. The studied birds were considered off-duty females as they were seen to enter the area from the breeding hills at the time of the morning changeover at nests (about 10:00 h), and by their diffuse plumage patterns. For data on plumage patterns in relation to sex and age, see Byrkjedal (1978b), Parr (1980).

The observations were made at 300–600 m, occasionally at a shorter distance, from a blind or a car. A 20–30× spotting scope and a tape recorder were used. When possible, data for both mates in pairs were recorded simultaneously; otherwise observation bouts of about 30 min were alternated between male and female. Observations on each pair or single bird were done for several hours in succession. I attempted to cover the daylight hours equally, but did not succeed (Appendix 1), as birds were easily disturbed.

Construction of a time budget.—Time budgets usually change during the day (Maxson and Oring 1980). Accordingly, in constructing a 24-h time budget for the different breeding stages I made the following assumptions: In the prelaying period I estimated two alternative time budgets by assuming (1) that the activity remained the same throughout the 24-h period; and (2) that the birds rested at night. In the incubation period off-duty females rested 3 h in the middle of the day. I lacked evening observations of such females, but I assumed that they engaged in the same activities as in the morning and afternoon. Off-duty male time budget is based on telemetric monitoring. The time not spent feeding was considered as alertness for the time budget estimation, as frequent alarm calls were heard. Just after hatching the females brooded through the night (telemetric monitoring), and I assumed they did so in the first week of the chicks' lives. Males' nighttime and daytime activities after hatching were considered to be the same, as vocalizations by a male were heard during the night from different directions, while I monitored his mate telemetrically. Probably, this somewhat overestimates his guarding activity and underestimates feeding, resting, and preening. When the chicks were 9–11 days old, the parents took a long midday and early afternoon resting period. Early morning and late evening activity frequencies were similar in both sexes, and I assumed the same activities over the night.

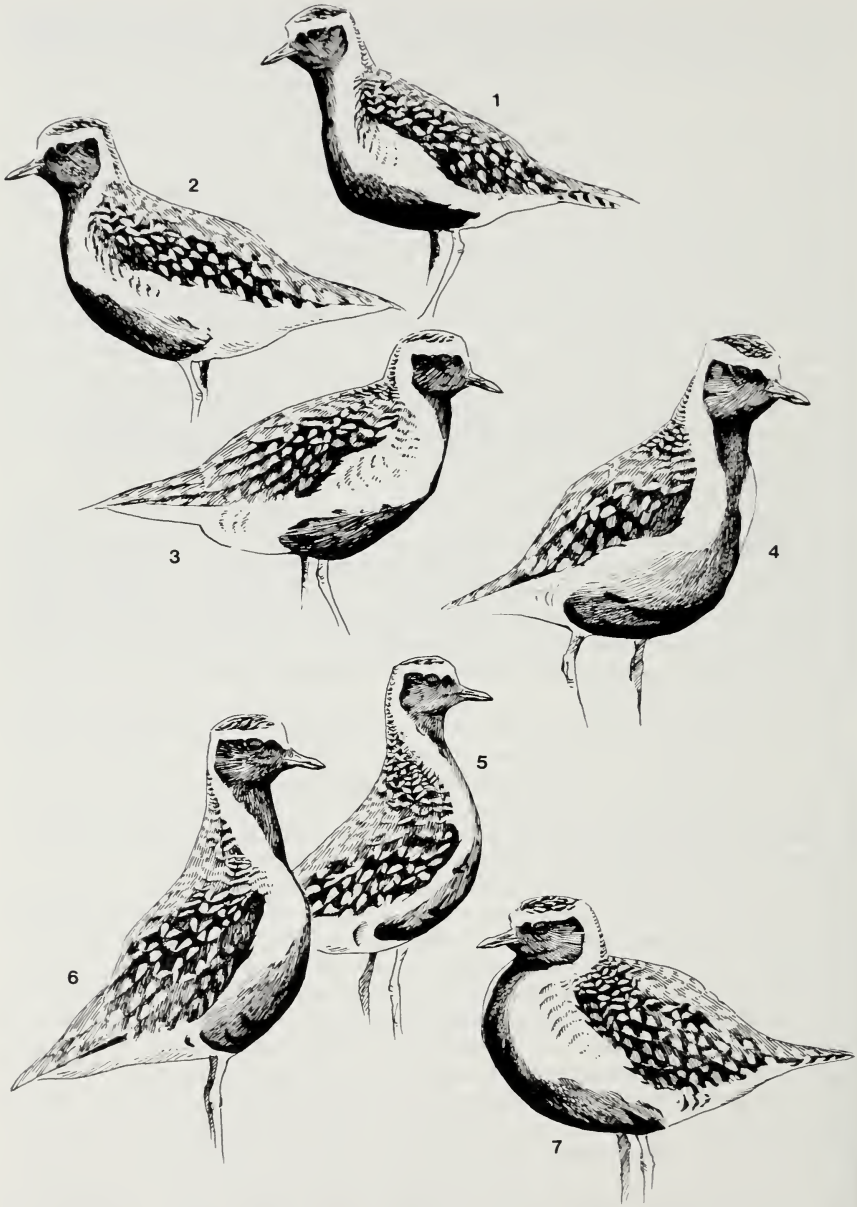

FIG. 1. Postures of Greater Golden-Plovers. 1–4 = non-alert postures, 5–6 = alert postures between pecks, 7 = relaxed posture.

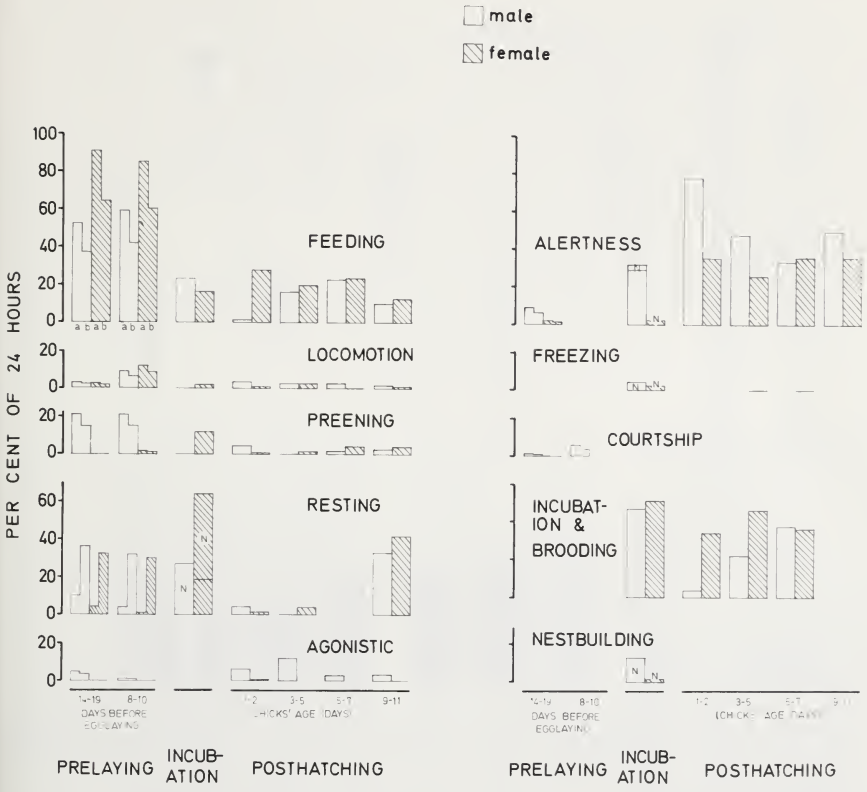

FIG. 2. Estimated frequencies of behavior patterns of Greater Golden-Plovers at different stages of the breeding cycle. Behavior at egg laying and hatching was not sampled. N = behavior performed on nest (all Ns add up to the percentage of time spent incubating). There are two alternatives in the prelaying period: (a) = daytime equals nighttime activities, (b) = nighttime activity (7 h) = resting. "Agonistic" includes both aerial display and chasing of intruders.

RESULTS

Prelaying activities.—Both males and females performed all their prelaying activities on the territory. The most time-consuming activity for both mates was feeding; in no other part of the breeding period was so much time spent feeding (Fig. 2). Females did little else but feed and rest. Males guarded the territory, stayed alert, performed aerial displays, and chased intruders. Only rarely did females chase away intruders. Usually they stood alert as the male did the chasing.

Although the males apparently found ample time for preening, their

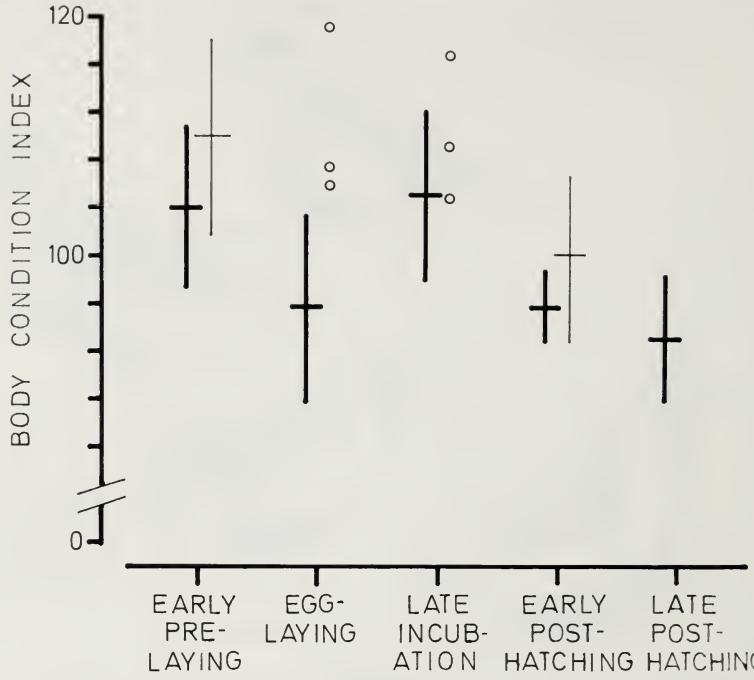

FIG. 3. Mean (±SD) body condition indices (100 × weight [g]/wing length [mm]) of males (thick lines) and females (thin lines) at different stages of the breeding cycle, sampled as follows (several years): Early prelaying: 11–15 May (22 males, 8 females), egg laying: 6–11 June (6 males, 3 females), late incubation: 30 June–10 July (6 males, 3 females), early posthatching: 22 July (9 males, 5 females), late posthatching: 16–18 August (17 males, 0 females). Circles = individual females.

body condition declined from prelaying to egg laying ($t = 2.4475$, df = 25, $P < 0.01$) (Fig. 3), indicating a high energy expenditure. During the prelaying period both males and females found most of their food on the surface and in the ground. During uninterrupted feeding bouts the pecking rate was about 2–3 pecks per min (Fig. 4).

Activities during incubation period: on the nest.—The parents shared the incubation duties about equally. The males were relieved on the nest by the females about 10:00 and the females by the males about 22:00 (Fig. 5). Thus, the sitting spells lasted for about 12 h. During incubation duty the incubating bird spent 1–2% of the time off the nest (Table 1). This sometimes coincided with herds of caribou (*Rangifer tarandus*) passing across the nest-site area, and was not considered to be feeding excursions. During a total of 18,054 min of machine recordings and visual observations at seven nests an overall nest attendance of 98.3% was found. (This does not include data from egg-laying or hatching periods.)

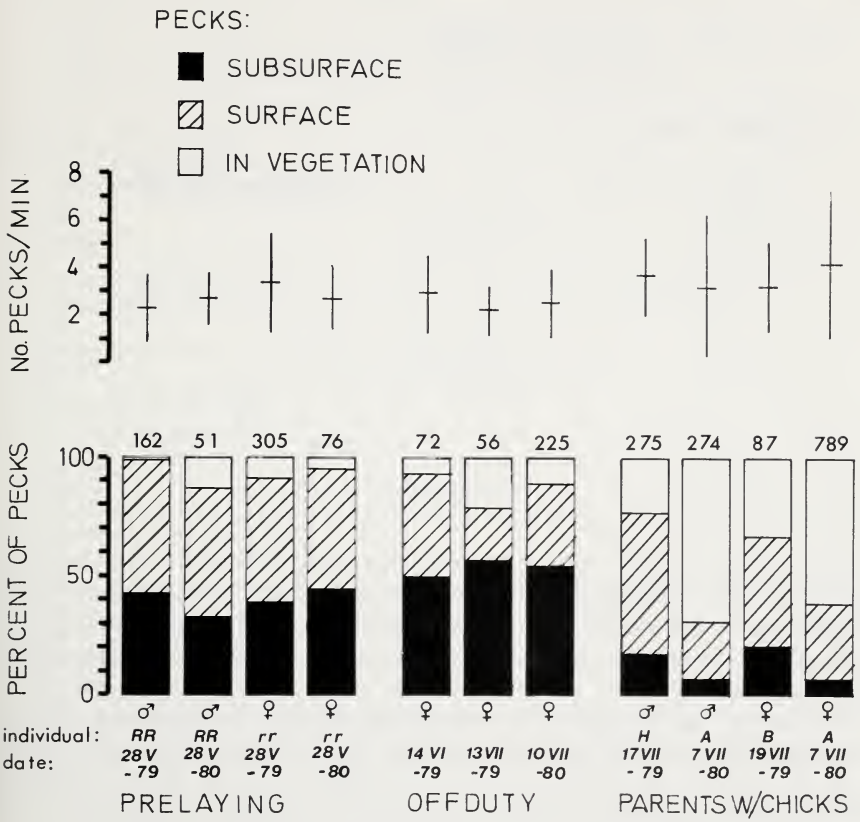

FIG. 4. Pecking rates and frequencies of pecks in the ground, on the surface, and in the vegetation by feeding Greater Golden-Plovers at different stages of the breeding cycle. Sample sizes (number of pecks) are given above the bars.

On the nest males spent about 58% and females 88% of the time relaxed (Fig. 2). The males especially engaged in throwing bits of straw and lichens into the nest. Both were occasionally alert and "froze" (squatted flat) when Common Ravens (*Corvus corax*) or Mew Gulls (*Larus canus*) flew over.

Activities during incubation period: off-duty.—In seven of eight observations of morning changeovers, females left the territories for distant areas where they fed extensively, rested, and preened (Fig. 2). Females were not seen on the territories when the males were incubating.

Observed changeovers (N = 8) in the evening did not reveal whether any of the males left the territories. Males may have been on territories in early morning and late evening when the females incubated, but their behavior was cryptic. From 21:30 to 00:15 on 16 and 17 July 1981, a

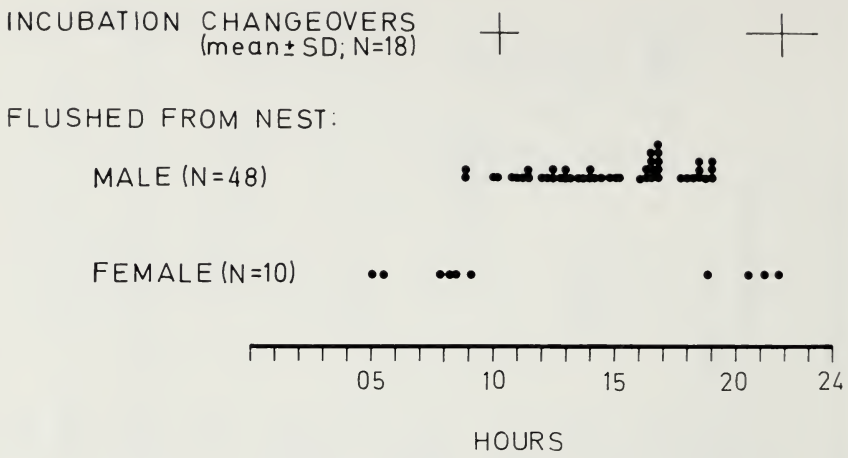

FIG. 5. Changeovers at nest.

radio-tagged male was on his territory, spending 30% of the time feeding, 30% of the time being active but not feeding, and 40% of the time standing still (Fig. 2). He left at 00:16 to feed nonstop, 1 km away, until 02:51, when he returned. Recording was terminated at 03:01; he was then active but not feeding.

Although mates shared the incubation equally, females rested about 62% and preened about 11% of the time, while males spent only 13% and <0.5% of the time in these activities. On the other hand, males were alert 31% of the time (based largely on telemetric recordings) compared to 1.5% of the time by females.

In the latter half of June, when most golden-plovers were on nests, the population showed a peak in the aerial display activity (Fig. 6) that was significantly higher than in the prelaying period ($\chi^2 = 4.9603$, df = 1, $P < 0.05$) but not significantly higher than in early posthatching ($\chi^2 = 2.3009$, df = 1, NS). I failed to record any such activity of the "focal males" during the incubation period. The radio-tagged male was studied at such a late date that most of the aerial display activities in the population had ceased.

In males, body condition increased significantly from egg laying to late incubation ($t = 2.0922$, df = 10, $P < 0.05$) (Fig. 3). The six females I weighed indicated that females also terminated the incubation in good condition (Fig. 3). Two of those weighed at egg laying were collected and had eggs in the oviduct.

The frequencies of pecks of off-duty females in June were similar to those in prelaying pairs in May (Fig. 4). In 1979, off-duty females in July, however, pecked significantly more often at the vegetation ($\chi^2 = 6.604$,

TABLE 1
NEST UNATTENDED, AS RECORDED BY MEANS OF THERMOGRAPHS IN FIVE NESTS[a]

	$\bar{x} \pm$ SD	Number of registrations
Number of times off nest per sitting spell:		
Male	1.82 ± 1.54	11 spells
Female	1.00 ± 1.08	13 spells
Duration of periods off during sitting spells (min):		
Male	10.70 ± 9.95	23 times
Female	7.19 ± 9.59	13 times
Duration of nest unattended during changeover (min):		
Morning	1.86 ± 1.98	12 cases
Evening	3.01 ± 3.41	17 cases

[a] Sitting sex according to data in Fig. 5.

df = 1, $P < 0.01$) and significantly less often on the ground ($\chi^2 = 5.738$, df = 1, $P < 0.02$) than they did in June. The off-duty females in July probed more often ($\chi^2 = 19.91$, df = 1 [1979], $P < 0.001$; $\chi^2 = 271.3$, df = 1 [1980], $P < 0.001$), and pecked less often on the ground ($\chi^2 = 8.873$, df = 1 [1979], $P < 0.01$; $\chi^2 = 1.009$, df = 1 [1980], NS) and on the vegetation ($\chi^2 = 2.361$, df = 1 [1979], NS; $\chi^2 = 180.7$, df = 1 [1980], $P < 0.001$).

Posthatching activities.—Fig. 2 gives the time budget of three pairs representing four sampled stages in the chicks' ages (1–2 days, 3–5 days, 5–7 days, 9–11 days). Observations later in the posthatching period were difficult to obtain, as birds with chicks gradually moved out of view, even when the observer was 300–400 m away.

In the first week after hatching both mates were engaged in guarding and brooding (Fig. 2). Males also engaged in territorial defense. Comfort activities (resting and preening) were reduced by both mates, and during 1–2 days after hatching, the male spent less than 1% of the time feeding. The time spent feeding by the female, however, did not seem to be affected by the presence of the chicks. In the chicks' second week comfort activities were at prelaying levels in male and above incubation level in female, and both mates had reduced the time spent guarding and brooding.

Both parents, when guarding or brooding chicks less than one week old, constantly emitted soft "peep" notes. These calls were impossible to hear beyond 100 m, but they were inferred from slight mandibular and gular movements. Calls did not occur when the chicks were 9–11 days old.

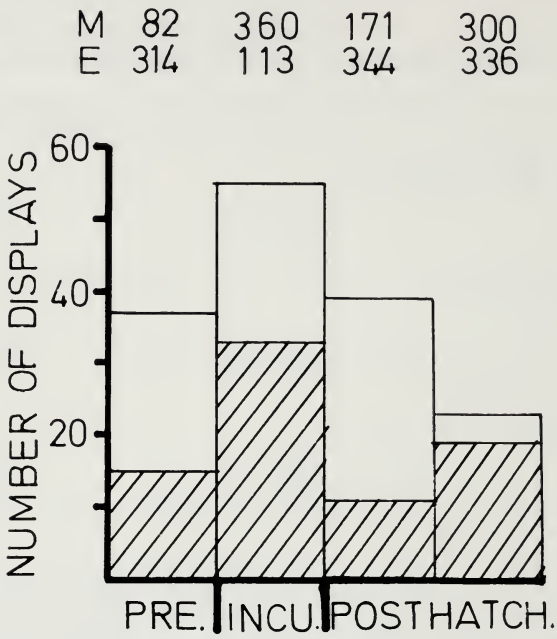

FIG. 6. Estimated number of aerial displays per 5-h morning observations (05:00–10:00, open bars) + 5-h evening observations (15:00–22:00, hatched bars), based on all displays recorded during observation bouts, not only those of focal birds. Observation time (min) is given above the bars (M = morning, E = evening). Data are from 1981; prelaying was sampled 20–22 May, incubation 11–17 June, early posthatching 28 June–7 July, mid-posthatching 8–14 July.

Simultaneously collected data on both mates showed that during the chicks' first week, and especially in their first 2 days, both parents rarely engaged in nonattentive activities before the other one had assumed guarding duties for a couple of minutes (except in 2 cases of 197 changes of activity). When the chicks were 9–11 days old, both mates most often engaged in nonattentive as well as attentive activities simultaneously (Fig. 7).

Even newly hatched broods were very mobile, and during the first few days broods were clearly far beyond the original nesting territory. Nevertheless, the male defended a large area around the brood. Attacks on conspecifics were elicited from about 100 m. On a few occasions the female took part in chasing as well. Both parents fed near the brood, except that a female, after having brooded without interruption for 5 h 25 min during the night, left for a 17-min feeding exodus (telemetric monitoring). During this feeding bout the male immediately took over the brooding and otherwise stayed close to the chicks.

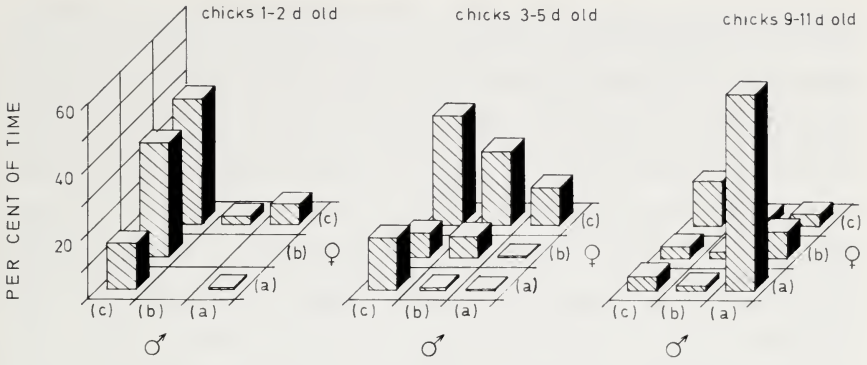

FIG. 7. Simultaneously recorded activities of mates at different posthatching stages. (a) = nonattentive behavior (feeding non-alertly, preening, resting, running, flying, aerial display, chasing), (b) = semiattentive behavior (alert feeding), (c) = attentive behavior (standing or running alertly, brooding). Left to right: Pair 6/81 28–29 June (345 min observations), pair 10/81 2–4 July (532 min observations), pair 6/81 8–10 July (529 min observations).

In males, body condition declined significantly in the course of the first week after hatching ($t = 3.4222$, df = 13, $P < 0.001$), but only slightly during the remainder of the posthatching period ($t = 1.1836$, df = 24, NS) (Fig. 3). In females, there might also have been a tendency for a rapid decline in body condition after hatching, as their body condition at that time was below that of early prelaying ($t = 2.1828$, df = 11, $P < 0.05$) (Fig. 3).

Parents with chicks found most of their food on the ground and in the vegetation, in contrast to prelaying pairs and off-duty females, which found their food chiefly on and beneath the ground surface (Fig. 4). Parents with chicks seemed to have a slightly, but not significantly ($t = 0.2500$, df = 200; $t = 0.2578$, df = 279), higher pecking rate than at other times.

DISCUSSION

Biparental care can improve (1) incubation efficiency, (2) nest and brood survival, and (3) mate condition to the extent it is important for reproductive success (Oring 1982). Here I discuss how biparental care in the Greater Golden-Plover affects these aspects.

Shared incubation enables the nest to be covered almost all the time. The high incubation constancy found in Greater Golden-Plovers is similar to that found in other shorebirds with shared incubation; in uniparental incubation the constancy is usually below 90% (Norton 1972, Ashkenazie and Safriel 1979, Maxson and Oring 1980, Kondrat'ev 1982, Löfaldli 1985). Low incubation constancy may increase incubation period (Pien-

kowski 1984) and thereby the risk of nest predation, but shorebird embryos may be quite tolerant to disruptions of egg-warming (Myhre and Steen 1979). In uniparental incubation there is more traffic to and from the nest than in biparental incubation (Norton 1972, Kondrat'ev 1982, Löfaldli1985), as conflicts between needs for self-maintenance and egg-warming select for many short feeding recesses, rather than few and long ones (Löfaldli 1985). In Greater Golden-Plovers there are about 120 passings to and from a nest during the incubation period, whereas in uniparental Eurasian Dotterels (*Charadrius morinellus*) breeding in the same area there are about 1400 (estimated from Wilkie 1981). Such traffic could make the nest more detectable to predators (Pienkowski 1984).

Shared incubation allows the golden-plovers time to seek good feeding sites far from their territories. The females' exoduses lasting almost all their off-duty time and the males' cryptic behavior when on territories while females incubate make Greater Golden-Plovers very unobtrusive during the incubation period (Kålås and Byrkjedal 1984b), which is apparently a part of their antipredator strategies. Although they perform distraction displays when flushed from the nest, they never chase predators by "dive-bombing" as do Black-bellied Plovers (*Pluvialis squatarola*) and Lesser Golden-Plovers (*P. dominica*) (Ratcliffe 1976; Sordahl 1981; Kondrat'ev 1982; Byrkjedal, unpubl.).

Close cooperation by the parents during the first week after hatching, when at least one of them is attentive at all times, is probably an efficient way to guard chicks. The time-activity budget and body-condition index show that tending in the early chick phase is very intense, while after 1½ weeks the parents are more relaxed and do not take turns to monitor the chicks continually. A similar change in development of parental care in the course of the posthatching period has been found in the biparental Killdeer (*Charadrius vociferus*) (Lenington 1980), some lapwings (Walters 1982), and Semipalmated Sandpipers (*Calidris pusilla*) (Ashkenazie and Safriel 1979), and may be common in shorebirds with biparental care. The behavioral change supports the idea that small chicks respond less rapidly to alarm calls, are more likely to go astray, and are less able to find good feeding patches than later on when they are more experienced (Lenington 1980, Walters 1982). Spotted Sandpiper (*Actitis macularia*), Killdeer, and Black-tailed Godwit (*Limosa limosa*) adults tending alone fed near normal levels, at the cost of constant chick surveillance (Maxson and Oring 1980, Lenington 1980, Byrkjedal 1985).

Weight loss during breeding in birds is common, and is usually considered indicative of a negative energy balance (e.g., Hussell 1972, Askenmo 1977, but see Norberg 1981 for a different view). In the Greater Golden-Plover the body condition index shows that incubation is an

energetically relaxed period, enabling the birds to regain physically from expenditures of territorial behavior, courtship, and egg laying, and to put on weight before the energetically demanding early posthatching period. Although Ashkenazie and Safriel (1979) considered incubation to be energetically costly for Semipalmated Sandpipers, their weights for incubating males, as well as weights for Dunlins (*Calidris alpina*) and Eurasian Oystercatchers (*Haematopus ostralegus*), indicate that in biparental incubation this may not be so (Holmes 1966, Mercer 1968, Soikkeli 1974). Even Spotted Sandpiper males incubating alone often gain weight, but their food situation is usually extremely favorable (Maxson and Oring 1980). Male Eurasian Dotterels in the same area as the present study lost weight when they incubated alone (Kålås and Byrkjedal 1984a); so weight gain in the incubating golden-plovers in spite of active molt over most of the incubation period (Byrkjedal 1978a) apparently was facilitated by shared incubation. Not only could individual golden-plovers seek good feeding spots far away, but they also had time to concentrate on favorable (subterranean) prey (see Byrkjedal 1980 for details on food). I suggest that holding of large territories in Greater Golden-Plovers (Nethersole-Thompson and Nethersole-Thompson 1961, Ratcliffe 1976, Parr 1980, Edwards 1982) and the intense early posthatching chick care would not be feasible without the energetic advantage from shared incubation.

Golden-plover territories apparently function chiefly to decrease nest and brood predation, as spacing prevails into the chick period, while feeding inside the territory takes place chiefly in the prelaying period. I have found a positive relationship between spacing and nest survival in this golden-plover population (Byrkjedal, unpubl.). Decreased nest predation with spacing of nests has also been documented for Snowy Plovers (*Charadrius alexandrinus*) (Page et al. 1983).

Why is it necessary for Greater Golden-Plovers to have large territories and highly intense chick care whereas the Eurasian Dotterel reproduces successfully in the same area and habitat and on the same food resources without these features? Maynard Smith (1977) presents a model showing how biparental care is selected for when it gives higher reproductive outcome than uniparental care of multiple clutches, and the chances for multiple matings are low. The difference between uniparental and biparental care is probably greater in golden-plovers than it would be in dotterels, as larger body size and four large vs three small eggs seem to make the former more detectable to predators (Byrkjedal, unpubl.). In the present study area, dotterels lose about 48% of the nests to predators (Kålås and Byrkjedal 1984a) compared to 78% in golden-plovers (Byrkjedal, unpubl.). Maxson and Oring (1980) considered that a high rate of nest predation could select for female emancipation in shorebirds, en-

hancing rapid replacement clutches, but as a prerequisite, one mate must be almost as good as two in caring for eggs and chicks (Maynard Smith 1977, Oring 1982). In Greater Golden-Plovers the prospects for successful uniparental care are probably very low, as four widowed females deserted their nests in less than 50 h after the loss of their mates.

SUMMARY

The time-activity budget of the Greater Golden-Plover (*Pluvialis apricaria*) was studied on a middle alpine breeding ground in southern Norway by means of visual focal-animal sampling, radio-tagging, and automatic incubation recorders. Body condition indices were obtained from shot and trapped birds.

Territory defense is mainly a male task. Large territories are maintained through the incubation period, and a similar-sized area around the brood is defended, although the brood leaves the nesting territory. By sharing the incubation (12 h daytime sitting spells in males, 12 h nighttime sitting spells in females) the birds feed extensively and improve their physical condition. This enables them to put maximum effort into periods of high energetic demands like prelaying territorial guarding, egg laying, and early posthatching guarding of chicks. Besides, off-duty exoduses from the nest area greatly facilitate unobtrusiveness during the incubation period. Close parental cooperation ensured constant guarding of newly hatched chicks; the intensity of chick-guarding declined in the course of 1½ weeks after hatching. It is suggested that biparental care in Greater Golden-Plovers is needed to cope with nest and chick predation.

ACKNOWLEDGMENTS

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Appendix 1

Distribution of Observation Time (Min)[a]

Category of bird	Date	Sex	Hours[b] 00:01–06:00	06:01–12:00	12:01–18:00	18:01–24:00	Obs. time (bird min)
Prelaying:							
3 pairs	28 May 1980	M	18	111	97	0	226
		F	0	80	113	0	193
3 pairs	19–22 May 1981	M	24	220	313	256	813
		F	24	220	262	258	764
Incubation:							
Off-duty							
1 bird	17–18 Jul. 1981	M	180[c]	0	—[d]	150[c]	330[c]
4 birds	10 Jul. 1980	F	—[d]	436	952	0	1388
On nest							
2 nests	11–17 Jun. 1981	M	—[d]	88	122	26	236
		F	17	293	—[d]	7	317
5 nests[e]	10 Jun.–8 Jul. 1981	M + F	4533	4235	4235	4498	17,501
Posthatching:							
Chicks' age (days)							
1–2 (Pair 6/81)	28–29 Jun. 1981	M	0	95	232	136	463
		F	0	81	251	62	364
3–5 (Pair 10/81)	2–4 Jul. 1981	M	30	101	254	192	581
		F	10 + 311[c]	88	319	184 + 223[c]	601 + 534[c]
5–7 (Pair A/80)	7–9 Jul. 1980	M	15	146	142	81	384
		F	26	163	203	17	409
9–11 (Pair 6/81)	8–10 Jul. 1981	M	20	146	273	216	655
		F	43	109	276	205	633

[a] Excluding time when birds were temporarily out of sight during observation bouts.
[b] Sunrise and sunset in the period 19 May–18 July were at 03:51–03:44 and 21:22–21:45, respectively.
[c] Monitored by radio telemetry.
[d] All incubation or off-duty in that period by the other mate.
[e] Monitored by thermograph.

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INTRASEASONAL MOVEMENT BETWEEN COLONY SITES BY CASPIAN TERNS IN THE GREAT LAKES

FRANCESCA J. CUTHBERT

Larids nesting in stable habitats tend to occupy the same breeding colony for many years, whereas those that occupy unstable environments shift colony sites frequently if nesting habitat becomes unsuitable (McNicholl 1975, Burger and Shisler 1980). The tendency of larids to return to the colony of previous breeding, providing environmental conditions remain favorable, is referred to as "site tenacity" (Austin 1949). Past studies on intercolony movement in the Great Lakes (Ludwig 1974, Morris and Hunter 1976, Southern 1977, Haymes and Blokpoel 1978, Southern and Southern 1979, Blokpoel and Courtney 1980) have focused on tenacity between seasons, but little is known about the movement of birds between colonies within a single breeding season. I examined seasonal colony site use patterns in Caspian Terns (*Sterna caspia*) nesting on five islands in northeastern Lake Michigan to answer the following questions: (1) do individual terns use more than one colony site during a single breeding season; and, if so, (2) what are the factors that influence intraseasonal colony site movement in this population?

STUDY AREA

During my study the resident Caspian Tern population in the Great Lakes was concentrated at 15 colony sites in the northern parts of lakes Michigan and Huron (the North Channel and Georgian Bay) and Lake Ontario. Shugart et al. (1978) estimated that the total 1978 Great Lakes breeding population was 3740 pairs. For logistic reasons I restricted my study area to five islands in northeastern Lake Michigan (Fig. 1). These colonies supported approximately 1100 pairs of Caspian Terns, representing about 30% of the Great Lakes population from 1976 to 1979. The colony sites were (1) the northeastern point of High Island, (2) High Island Shoal, (3) Hat Island, (4) Shoe Island, and (5) Ile aux Galets. Distance between colony sites ranged from 1 to 39 km (Table 1).

Colony site habitat in the Great Lakes varies in stability. The lakes are characterized by fluctuating water levels (Cohn and Robinson 1976), and these changes determine the quantity and quality of sites available to terns in each season (Shugart et al. 1978, Cuthbert 1981). When the lake level is above average, Shoe Island is submerged or so reduced in size that it is unsuitable as a breeding site. High Island Shoal also is unavailable for breeding by terns except when the water level is below or near average. The level of Lake Michigan in the month of June was above average for all years of this study except 1977 (U.S. Army Corps of Engineers, 1976–1979). Caspian Terns nested on High and Hat islands and Ile aux Galets during all four years of this study, on Shoe Island during 1977–1979, and on High Island Shoal in 1977. Historical records for this region (Hatt et al. 1948) suggest that a local population tends to use the same colony sites from year to year. However, because terns

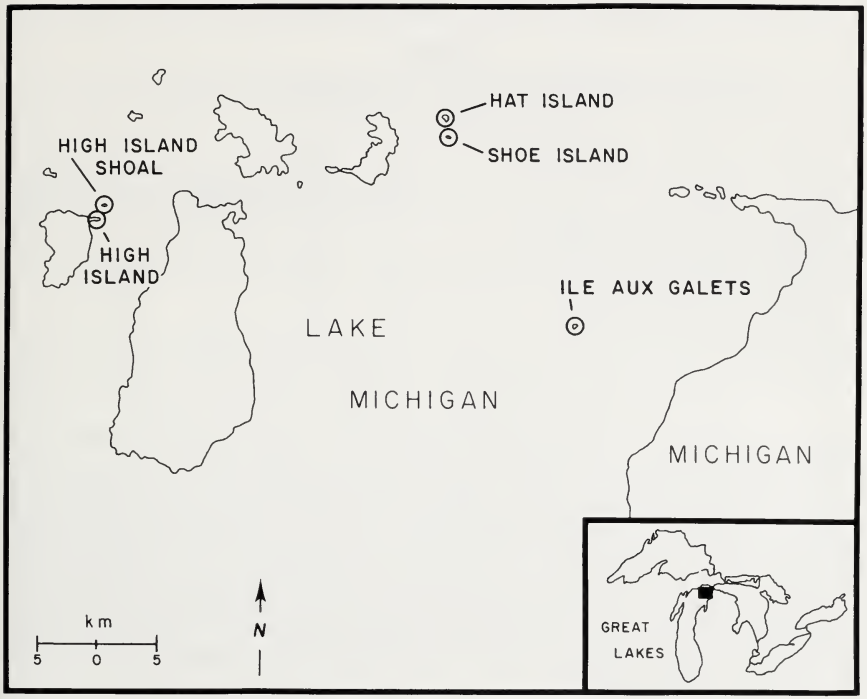

FIG. 1. Study area in northeastern Lake Michigan.

were not color marked until my study, these earlier records indicate colony site use by the breeding population and not for specific individuals. A preference for traditional colony sites is indicated for the rest of the Great Lakes population as well (Ludwig 1962, 1965; Blokpoel and Fetterolf 1978).

METHODS

Data were collected during the breeding season (mid-April to mid-August) from 1976 through 1979. The islands were reached by float plane or boat; I visited the colonies on a rotational schedule every 3–7 days throughout each season. When I was not present, supplemental observations were made by investigators on High, Hat, and Shoe islands.

Capturing and marking techniques.—From 1976 to 1978, I captured and color marked 330 adult Caspian Terns. Initially, I used a cannon net (Southern 1972) to capture 254 terns (125 at Hat Island and 129 at Ile aux Galets). These birds were tagged with individually numbered vinyl-coated nylon patagial wing markers (Southern 1971) that were color-coded to colony site. After I observed that intensive cannon netting caused incubating terns to desert their nests (Shugart et al. 1978), I changed capture techniques. In 1978 an additional 76 adults were captured with a monofilament line nest snare (28 on High Island and 48 on Ile aux Galets) and banded with unique combinations of colored plastic leg bands. All adults also were banded with a USFWS leg band. To monitor the reproductive status of adult terns, I banded chicks with USFWS and plastic leg bands.

TABLE 1
DISTANCE (IN KM) BETWEEN CASPIAN TERN COLONY STUDY SITES IN NORTHEASTERN LAKE MICHIGAN

	High Island	High Island Shoal	Hat Island	Shoe Island	Ile aux Galets
High Island (45°45′N, 85°40′W)	0				
High Island Shoal (45°45′N, 85°40′W)	1	0			
Hat Island (45°47′N, 85°18′W)	28	27	0		
Shoe Island (45°48′N, 85°18′W)	28	27	1	0	
Ile aux Galets (45°41′N, 85°11′W)	38	39	18	17	0

Intercolony movements.—From 1977 to 1979, I spent 1–6 h/day (>1200 h total) locating marked individuals at the Ile aux Galets and High Island colony sites. Observation time was divided equally between both sites. I spent 120 h looking for marked terns at Hat Island in 1977 and 1978 and 20 h on Shoe Island from 1977 to 1979. G. Shugart recorded marked individuals on Hat and Shoe from 1977 to 1979. I was unable to look for marked birds on High Island Shoal in 1977 as all terns took flight when the colony site was approached by boat. Therefore, the best data on intercolony movement are from the Ile aux Galets and High Island sites. Data collected on marked terns at each encounter included status (nesting, not nesting) and stage in the reproductive cycle (courtship, nest construction, incubation, chicks present, postnest failure).

Determination of reproductive status.—To examine the relationship between reproductive status and intercolony movement, I studied the nesting phenology of all color-marked terns at High Island and Ile aux Galets in 1978 and 1979. G. Shugart recorded reproductive status of marked birds observed on Hat Island. Nests were numbered and periodic inspection of their contents was made every 3–4 days from early incubation through banding of chicks. After chicks were marked, I observed color-marked parents and their offspring from blinds on the edge of the colonies to minimize disturbance. Causes of reproductive failure (e.g., storm washout, investigator disturbance, gull predation, unknown factors) were recorded during nest checks. Although both members of some pairs were color marked, data were collected and analyzed for individuals. Data on reproductive status and intercolony movement were analyzed using a chi-square test (Zar 1974).

RESULTS

Intercolony movements.—During each of three years of observation, two patterns of colony-site association emerged (Table 2): (1) 46–65% of the marked terns were observed at one colony site for the entire breeding season; and (2) 34–63% were recorded at one colony site for only part of the breeding season. The behavior of birds in the second group could be subdivided as follows: (1) 18–26% were noted at one site for part of the breeding season and then disappeared for the remainder of the summer; and (2) 16–37% were present in the breeding area all summer but were

TABLE 2
NUMBER OF CASPIAN TERNS OBSERVED AT MORE THAN ONE COLONY IN 1977–1979

	1977 (N = 220)	1978 (N = 114)	1979 (N = 68)
Observed at one colony for entire season	126 (57)[a]	74 (65)	31 (46)
Observed at one colony for brief period	58 (26)	22 (19)	12 (18)
Observed at more than one colony	36 (16)	18 (16)	25 (37)

[a] Percent of total.

seen at two or more active colony sites. These data indicate that intercolony movements occur regularly in this population of terns.

Causes of intercolony movement.—To determine factors that affect the movement patterns of terns, I categorized birds observed at two or more sites according to their reproductive status: (1) nesting birds with eggs or chicks, or (2) terns that were not nesting. Combining data from 1978 and 1979 (Table 3), I found that at the time observations were made 38 (88%) of the birds recorded at two or more sites were not nesting and only 5 (12%) had eggs or chicks at another colony site. When I examined reproductive status of marked birds observed at only one colony site for the entire season, I found that 98 (93%) were nesting birds and 7 (7%) were not nesting. Using 2 × 2 contingency table analysis, I tested and rejected ($\chi^2 = 96.23$, df = 1, N = 148, $P < 0.001$) the hypothesis that intercolony movement is independent of reproductive status. Terns with eggs or chicks associated almost exclusively with one breeding colony, and intercolony movement was most likely to occur in birds that were not breeding.

A more detailed examination of individuals observed at two or more sites showed that of the birds that were not nesting (N = 38), 55% had experienced reproductive failures earlier in the same season, 34% were involved in courtship or nest-site selection behavior, and 11% were nonbreeders for the entire season. Therefore, intercolony movement was precipitated by lack of a mate or nest site and by reproductive failure.

Observations on the 34 terns recorded for only part of the season at one site that subsequently disappeared for the duration of the summer (1978, 1979) provide further information on intercolony movement in this population. Twelve (35%) were courting for one to several days at one site during late April or early May. Another 12 (35%) were breeding birds that deserted the site following investigator disturbance or destruction of the nest contents by gull predation or storms. None of these individuals was recorded again for the duration of the season. Lastly, 10

TABLE 3
REPRODUCTIVE STATUS OF INDIVIDUALS OBSERVED AT MORE THAN ONE COLONY IN 1978 AND 1979

	Percent of total (N = 43)
Terns that experienced reproductive failures	49
Unpaired terns involved in prenesting activities	30
Terns with eggs or chicks	12
Terns that were unpaired for entire season	9

terns (29%) that were observed briefly after early June all behaved as if they had lost eggs or chicks (i.e., stood on colony edge with a mate, performed nest site selection behavior, attempted to feed unrelated chicks). Some or all of these individuals may have finally nested at colony sites outside the study area.

Intercolony movement by birds involved in courtship or nest-site selection tended to be temporary, as most individuals eventually obtained a mate and chose a nest territory at a specific colony site. When actively searching for a mate, terns courted at the colony site of future nesting, at other active colony sites, or at communal resting spots such as sand bars or stretches of undisturbed beach along the shoreline of northern Lake Michigan. Some individuals visited several colony sites a day until they acquired a mate. Individuals often constructed a few nest scrapes with temporary partners; however, once an individual began to associate with an exclusive mate, the pair made many trial nest scrapes at from one to several colony sites in the study area. Once the nest was constructed and egg laying initiated, terns were rarely observed at colonies other than the one where they were breeding unless the reproductive effort was interrupted by prolonged disturbance or destruction of the nest contents.

During this study reproductive failures were caused by storms (55%) and gulls (3%) that destroyed nests, eggs, or chicks, and investigator disturbance (22%) that led to nest desertion. Unknown factors accounted for 20% of the failures. The typical response of terns to destruction of the nest or its contents was to remain in or adjacent to the nest territory for 2–7 days. After this time they usually deserted the colony and often renested at another colony or associated with several colonies as nonbreeders for the remainder of the summer; occasionally, individuals remained and renested at the original colony.

Insight into the impact of prolonged investigator disturbance on intercolony movement is provided by the results of an isolated incident in

1977. Approximately two-thirds (445 pairs) of the Caspian Tern colony deserted the Hat Island site after cannon netting activities in early June (Shugart et al. 1978). Eighty-one terns had been tagged with individually numbered wing markers. After the disturbance, 24 of the tagged birds continued to nest on Hat, 20 left Hat Island and either renested (11) or were observed (9) at High Island or Ile aux Galets, and 37 deserted Hat Island and were not recorded for the duration of the breeding season.

DISCUSSION

Intraseasonal movement of terns between colonies in northeastern Lake Michigan was common. The most accurate estimates are probably reflected in the 1979 data, as no new birds were marked during this season and no patagial-tag or color-band loss was known to occur. In addition this was the only season when extensive observations were made on color-marked individuals during the pre-nesting stage, a period when birds move between sites before selecting a mate and nest location.

In the area studied, intercolony movement within a season is probably confined primarily to the islands in northeastern Lake Michigan; however, terns may move to the colonies outside of this area but still within the range of the Great Lakes population. Color-marked birds occasionally disappeared after they were observed courting in early spring, and eventually may have nested on Gravelly Island, in northwestern Lake Michigan, or in one of the Canadian colonies. Ludwig (1968, 1980) reported some interseasonal movement of individuals between the lakes Michigan and Huron colonies but found a greater tendency of terns from the Canadian colonies to disperse to the Lake Michigan colonies than the reverse situation. I found that 8% (N = 119) of the previously banded birds captured during my study were banded at colonies in Lake Huron (Cuthbert 1981).

Documentation of intercolony movement is difficult to obtain because it requires (1) individually marked birds and (2) investigators to find them by regular visits to many or all colony sites within the range of a breeding population. Austin (1949) not only found that Common Terns (*Sterna hirundo*) often desert a colony site after experiencing reproductive failure, but he also established that these birds renested at other colonies within the Cape Cod area. Buckley and Buckley (1972) noted that some Royal Terns (*S. maxima*) deserted their breeding colony in response to color-banding activities and subsequently were observed at an adjacent colony site. Finally, Southern (1977) reported wing-marked Ring-billed Gulls (*Larus delawarensis*) at colony sites different from the one where they were captured earlier in the season but stated that reasons for intercolony movement were unknown.

In this study intercolony movement was recorded most frequently in terns that experienced reproductive failure. Similar patterns of intraseasonal intercolony movement may also occur in other populations of Caspian Terns as well as in other species of larids that breed in areas where alternative colony sites are available and reproductive failures occur frequently. Other investigators have documented terns deserting eggs or chicks in response to disturbances of breeding adults or destruction of nest contents. Examples include predation (Austin 1944), ectoparasites (Feare 1976), storm damage (Austin 1949, Hardy 1957), and human disturbance (Bergman 1953, Vaisanen 1973, Shugart et al. 1978).

Because courtship behavior in Caspian and other species of terns (e.g., Common Tern, Austin 1947; Sandwich Tern [*S. sandvicensis*], Langham 1974; Royal Tern, Buckley and Buckley 1972) may be performed at locations other than the breeding colony, some movement between colonies probably occurs wherever populations are divided into subgroups of individuals that breed at two or more colonies within a specific geographic area.

During the study period the most frequent cause of reproductive failure in this population was nest destruction due to storm damage (Shugart et al. 1978, Cuthbert 1981). This suggests that intercolony movement by individuals breeding in northeastern Lake Michigan probably is greatest during years of higher than average lake level. High water levels may also increase movement of birds during the courtship period. Although Caspian Terns from the Great Lakes population exhibit site tenacity to the colony of previous breeding (Cuthbert 1981), birds that return to a colony and find it submerged as a result of high lake levels will be forced to breed at a new location. Under these circumstances individuals may be less likely to pair with their mate from the previous year (Cuthbert 1985) and may visit several colony sites searching for a new mate.

Results of the present study suggest that unless extensive observations have been made on marked individuals, colony sites located within the local range of a breeding population should not be viewed as independent demes either within or between seasons. Because information on demographic patterns is essential to understanding the biology of colonial species, knowledge of the extent and causes of intercolony movement is important to investigators studying populations in which it is common.

SUMMARY

Colony-site use patterns were studied in Caspian Terns (*Sterna caspia*) nesting on five islands in northeastern Lake Michigan to address the following questions: (1) do individual terns frequent more than one colony site during a single breeding season; and (2) what are the factors that influence intraseasonal colony site movement in this population?

Intraseasonal movements of terns between colonies in northeastern Lake Michigan were common. Birds that were not nesting were observed significantly more often at two or more colonies than nesting terns, and intercolony movement was precipitated by lack of a mate or nest site and by reproductive failure (e.g., nest destruction by storms or predators and investigator disturbance). Intercolony movement during courtship and following reproductive failures probably is intensified during periods of flooding or high water in the Great Lakes.

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MOVEMENT OF MOJAVE DESERT SPARROW FLOCKS

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Cody (1971) attributed nonrandom movement in bird flocks in the Mojave Desert to selective benefits from increased foraging efficiency. By intensive nonrandom searching in a group, birds increase the patchiness of their food, making it easier for them to find previously unforaged areas and to avoid depleted areas (Cody 1971). Although evidence suggests that flocking improves foraging efficiency in birds (Moriarty 1976, 1977; Morse 1977), the general applicability of Cody's observations on desert sparrow flocks remains largely untested (see Morse 1980:276). In this study, we examined the movement of sparrow flocks in the Mojave Desert in an attempt to replicate Cody's observations. We also studied the movement patterns of water courses (e.g., washes, arroyos) because our observations indicated that the flocks might be following these topographical features. If flocks follow water courses and water moves nonrandomly, then nonrandom flock movements may not be the result of selection as described by Cody (1971), but rather a result of the terrain through which the flocks move.

METHODS

The study area was approximately 25 km S of Barstow, San Bernardino County, California, at an elevation of 653 m. The site is dominated by a central ridge with a bajada sloping gently away from the ridge to the north and the south. The terrain is broken up by occasional washes and arroyos. Perennial vegetation is dominated by creosote (*Larrea tridentata*) with some Mojave yucca (*Yucca schidigera*) and Joshua tree (*Yucca brevifolia*) present on the south slope.

Observations on flocks were made from January 1979 to March 1979 and from December 1979 to March 1980 at various times during the day. Twenty-four flocks were observed for a total of 1213 min. A flock was defined as a cohesive group of individuals moving together and reacting to social cues from one another (Moriarty 1976, Morse 1980). Typically, flocks moved in short flights between feeding sites. Data taken on each flock included: (1) flock size and composition—the estimated total number of individuals and species; (2) flock velocity—the rate of movement as estimated by the total distance moved during the total time observed; (3) time at feeding sites—the average time spent at feeding sites while the flock was observed; (4) distance between feeding sites—average distance of all straight-line flight segments between feeding sites; and (5) path directionality—estimates of the tendency for flocks to turn in various directions (explained below). To determine path directionality, we followed each flock at a distance of 40–70 m, a distance at which the birds did not appear to be disturbed. Care was taken not to flush or "drive" the flock. All distances were paced or estimated by a single observer (JE).

Path directionality involved mapping the progress of each flock. When the flock left a feeding site, the angle (to the nearest 10°) to the next feeding site was estimated using a compass. These maps were later used to score directionality between two straight sections

of path. The probability of a flock moving forward, backward, right, or left was calculated by dividing the path directionality score for that direction by the total of all path directionality scores for the flocks.

For example, suppose a flock is followed through three feeding sites, designated A, B, and C in the order visited. Further suppose that the angle between A and B is 110° (from north) and the angle between B and C is 90°. The turn at point B is scored in the following manner. The flock turned at an angle of 20° (110° − 90° = 20°) when leaving site B resulting in a score of 20 to the left. As the turn was in the left, forward quadrant, and the turn was 20° to the left, the remainder of the direction in the quadrant (90° − 20° = 70°) results in a score of 70 to the forward direction. This method is the same as that used by Cody (1971) except that Cody assigned a score of 90 to forward each time a straight section of path passed a 100-ft mark. We did not score any additional forward movement and scored only turns to avoid bias in favor of the forward direction.

In order to determine if water courses move in a nonrandom manner, we measured the directionality of water courses by the same method used for the bird flocks. We selected 12 water courses by starting in the middle of the study site and moving in the four cardinal directions. The first three obvious water courses (arroyos or washes) encountered in each direction were measured. Because water courses did not have "feeding sites," we defined seven functional sites at a distance of 42 m apart and measured directionality as explained above. We used seven sites at 42 m because these were the averages for these variables in the 24 flocks.

Tests for significant differences between two sample means were done using the t' procedure (Sokal and Rohlf 1969). Equality of more than two means was tested using analysis of variance. Multiple comparisons were accomplished by two-sample t-tests using Bonferroni probabilities. All directional probabilities were arcsin-transformed before statistical testing.

RESULTS

Birds observed in flocks included the resident Black-throated Sparrow (*Amphispiza bilineata*) as well as wintering Sage (*A. belli*) and White-crowned (*Zonotrichia leucophrys*) sparrows. Twelve of 24 flocks observed during the two seasons were comprised of a single species. Sage Sparrows comprised eight of the single-species flocks, White-crowned Sparrows comprised three, and Black-throated Sparrows comprised one. Sage and Black-throated sparrows were involved in seven two-species flocks. Sage and White-crowned sparrows were in one flock together. Black-throated and White-crowned sparrows were in one flock together. All of the single-species flocks were seen during the 1980 field season.

Flocks progressed in a rolling motion from one feeding site to the next with 1–3 individuals (usually Sage or Black-throated sparrows) leading the group. Feeding sites for an entire flock were usually no larger than 100 m^2. Separate flocks were never observed intermingling.

If the directional movement of flocks was random, we would expect equal probabilities for forward, backward, right, and left turns. Average probabilities for the four directions (Table 1) were not equal ($F = 82.3$, $df = 3,92$, $P < 0.0001$). Multiple comparisons analysis indicated that the

TABLE 1
CHARACTERISTICS OF FLOCKS OF BIRDS AND WATER COURSES ON THE MOJAVE DESERT

	Flocks		Water courses
	This study N = 24	Cody (1971) N = 14	This study N = 12
No. species	1.7 ± 0.8	3.2 ± 0.9	
No. individuals	18.8 ± 10	68.0 ± 40	
Flock movement			
Velocity (m/min)	0.10 ± 0.04	0.09 ± 0.02	
Forward	0.61 ± 0.21	0.69 ± 0.13	0.85 ± 0.03
Right	0.20 ± 0.15	0.15 ± 0.09	0.07 ± 0.03
Left	0.18 ± 0.13	0.13 ± 0.07	0.08 ± 0.03
Reverse	0.02 ± 0.04	0.03 ± 0.04	

probability of moving forward was the largest, that there was no significant difference between the probabilities of turning right or left, and that the probability of reversing was the smallest. Flocks showed a definite tendency to move in a forward direction.

Comparison with Cody (1971).—Our study site was located about 130 km to the southeast of Cody's (1971). Both areas were in the Mojave Desert, and vegetation and topography appeared to be similar. The principal difference between the two studies is the size and composition of the flocks studied (Table 1). Flocks in our study had fewer species and individuals than did the flocks Cody observed, and his flocks varied more in the number of individuals, although coefficients of variation are similar.

There was no significant difference between flocks we observed and those observed by Cody in the velocity at which they moved (Table 1). All of the directional probabilities were the same for flocks we observed and those reported by Cody (Table 1). An analysis of variance of Cody's probabilities showed significant differences ($F = 197.7$, df = 3,52, $P < 0.0001$) among the means for the four directions. Multiple comparisons indicated that the forward probability was the largest, that there was no difference between the left and right probabilities, and that the probability of reversing was the smallest. In other words, although our flocks were smaller than Cody's their movement patterns were similar.

Comparison to water courses.—The probability of water courses moving forward (Table 1) was greater than the probability of our flocks moving forward ($t' = 5.5$, $P < 0.01$), while the probability of water courses going left or right (Table 1) was less than the probability of our flocks turning left or right (left, $t' = 3.6$, $P < 0.05$; right, $t' = 4.1$, $P < 0.05$). Water

courses never reversed (Table 1). The probability of our flocks turning back was significantly different from zero ($t' = 2.4$, $P < 0.05$).

Analysis of variance and multiple comparisons on water course probabilities resulted in the same pattern seen in our and Cody's flocks, i.e., the means for the three directions (reverse was excluded because there were no reversals) were significantly different ($F = 2070.9$, df = 2,33, $P < 0.0001$). Forward had the highest probability with no difference between left and right probabilities. The probabilities for forward, left, and right were significantly different from zero, the only value that can be assigned to the probability of water courses turning back.

DISCUSSION

Water course directionality is similar to flock movement, i.e., predominately forward with no difference between left and right turns, and reverse movement being very rare. The higher probability for movement ahead and lower probabilities of left and right turns for water courses as compared to flocks are likely a result of the greater degree of freedom of movement in birds. Although water courses are completely constrained by topography and gravity, birds have considerably more flexibility. Even if they generally follow a water course, flocks may move from course to course. While standing in one wash we could often see another wash easily, and if a flock "switched" washes it could result in a substantial turn, perhaps even a reverse movement. Therefore, although the exact probabilities of turns are different, we conclude that the overall pattern of sparrow flock movement is very similar to that of water courses. We suggest that sparrow flocks generally move forward, occasionally to the left or right, and rarely reverse, because they follow major features of local topography.

The distribution of seeds and shrubs is probably influenced by water flow (Brown et al. 1979), and following water courses may be the simplest way for birds to find these resources. We agree with Cody (1971, 1974) that flocks tend to avoid crossing over their own paths. We disagree that this movement is the result of selection for optimization behavior, and we offer the alternative explanation that the movement is a natural consequence of following the local terrain. We base this conclusion on our observations of flocks and on our data showing that the pattern of water course directionality is similar to flock movement directionality.

Even if flocks move nonrandomly because they follow water courses, it is unclear why birds should join flocks rather than forage alone. We suggest that predation rather than return-time regulation may explain the tendency of desert birds to flock. Cody (1971) dismissed predation as a factor influencing flock formation because he never saw a flock attacked. American Kestrels (*Falco sparverius*) and Golden Eagles (*Aquila chrys-*

aetos) were the only avian predators present in Cody's study, and he felt it unlikely that they would attempt to take a sparrow-sized bird. We believe that predation should not be dismissed. American Kestrels have been observed taking flocking Brewer's Sparrows (*Spizella breweri*) in Arizona (M. Marshall, pers. comm.), and their diet often includes small birds (Bent 1938, Craighead and Craighead 1956). We regularly saw Loggerhead Shrikes (*Lanius ludovicianus*) on our study area, and their diet often includes small birds (Bent 1950). Reynolds (1979) observed two successful kills each of Brewer's and Sage sparrows by Loggerhead Shrikes, as well as 23 unsuccessful attempts on these species within two years in Idaho. We observed a Prairie Falcon (*Falco mexicanus*), a predator not mentioned by Cody (1971), unsuccessfully attack a flock of eight Sage and Black-throated sparrows. Caraco (1979) demonstrated that flocking Yellow-eyed Juncos (*Junco phaeonotus*) scan less often for predators and increase foraging rate as flock size increases.

Although the frequency of attempted acts of predation may be small, nevertheless they may have played an important part in the development of flocking behavior through evolutionary time. Flocks may detect predators earlier than individuals (Powell 1974, Siegfried and Underhill 1975), as well as provide a place for individuals to hide (Hamilton 1971) and confuse the predator (Powell 1974). The tendency for flocks not to form in years of abundant resources (Cody 1971) might also be predator related, as exposure to predators would be reduced when less time was spent searching for food.

SUMMARY

The movement of 24 sparrow flocks on the Mojave Desert during two winters (1979–1980) was studied. The average flock had 19 birds of two species. Flocks moved nonrandomly with a definite preference for the forward direction. Left and right turns occurred with the same frequency, and reversals were rare. A comparison with Cody's data (1971) indicated that although our flocks were significantly smaller and contained fewer species, they were identical to his in all aspects of movement. We measured the paths of water courses (washes and arroyos) by methods similar to those used to measure flock movement. Water courses show a similar pattern of movement, i.e., most often forward, followed by right and left turns at equal frequency. Water courses did not reverse. Flocks we observed appeared to follow water courses. We conclude that flocks tend to follow water courses.

We suggest that Mojave Desert sparrow flocks form in response to predator pressure and move in nonrandom paths because they follow local topography. We feel flocking may result in increased foraging efficiency, but that it is not necessary to invoke complex optimization models (Cody 1971, 1974) to explain their formation and behavior.

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SURVIVORSHIP IN THE TUFTED TITMOUSE

WILLIAM H. ELDER

Most authors consider the Tufted Titmouse (*Parus bicolor*) a permanent resident species, but Van Tyne (1948) and Wilford (1977) distinguished transient and resident members of their banded populations of Tufted Titmice, and Condee (1978), using a moving trap-grid, found that so-called transients may have simply moved to an adjacent winter range to settle for breeding.

Compared with the Black-capped Chickadee (*P. atricapillus*) (Elder and Zimmerman 1983), there seem to be few published records of longevity in North American titmice and no studies of their population dynamics. A maximum longevity of 13 years 3 months was reported from a sample of 4460 recoveries received by USFWS (Clapp et al. 1983). The present analysis of 15 years of observations at a feeding and banding station was undertaken with the following objectives: (1) to use sightings of color-banded birds to estimate survival rates, (2) to compare these with estimates based on USFWS band recovery information, (3) to record maximum longevity and year-to-year site fidelity, and (4) to discern whether or not the species is migratory.

MATERIALS AND METHODS

The study was conducted at my residence near the city limits of Columbia, Missouri, where observations were recorded nearly every day for 15 years, 1965–1979. Sunflower seed was provided on a feeding shelf at a second-story level 4 m above ground level, and birds were watched for an hour after seed was put out in early morning and at noon.

When an unbanded bird was sighted, food was restricted the next weekend, and Potter (Lincoln 1929) or McCamey (McCamey 1961) traps were set. All trapped birds received a USFWS aluminum band on one leg and colored plastic bands (red, orange, yellow, green, blue, black, and white) on the other. After all the possible combinations had been used, an additional color band was used above the aluminum band to provide another series. No loss of color bands was found during the entire 15-year period.

Birds were observed daily, but the presence of each was tabulated on a weekly basis. New birds were caught usually within a few days; recaptures were recorded to permit analysis of trapability and frequency of repeated captures. Birds were not weighed, measured, or sexed. In summer, HY (hatch year) birds can be distinguished by mouth color (Wood 1969), but so few birds were present or trapable at this time that the numbers were not sufficient to be treated as a separate cohort for analysis. Most trapping was accomplished from September until birds dispersed in April.

At the end of 15 years, data were analyzed with the Statistical Analysis System (Helwig and Council 1979) for survival, trapability, seasonal presence, and consistency among years.

Banding and recovery data for the entire range of the species were supplied by the USFWS Bird Banding Laboratory, and data from 1959–1979 were analyzed for survival and movement.

RESULTS AND DISCUSSION

I banded 258 Tufted Titmice; of these, 238 were resighted or retrapped. There was no evidence of migratory movement; birds seen only once were taken in each month of the year. Twenty birds were never seen again after being retrapped once; their dates of arrival were scattered from August to March.

Arrival and departure.—New birds were trapped in every week from August through March but most frequently in November (28% of the total). A few birds were retrapped the next day but mean time to recapture was 3.8 weeks (SD = 4.7, N = 160). Only 20% of December arrivals stayed through January; 33% of January arrivals stayed through February. Local movement and concentrations at feeders were often associated with storms or prolonged cold. On the average, birds remained and were seen regularly for 18 weeks (SD = 9.6, N = 508). The length of their stay did not change with age. The mean span of time birds were absent before being seen again at the feeder was about 4 weeks; most absences were much shorter, but one bird stayed away for 26 weeks before returning the same year.

Trapability.—Birds were retrapped from 1 to 24 times in any one year, but 103 (43%) titmice were recaptured only once per year. One titmouse was captured 56 times during 5 years.

Sixty-two percent of the 258 titmice banded were retrapped and 92% were resighted. This difference is a measure of the frequency with which many birds enter traps to feed but escape without being caught. Many individuals became very proficient at hopping over the trap treadle without tripping the trap or flew so quickly that they escaped while the trap door was dropping.

Site-fidelity.—During 632 bird-years, 49 birds (7%) were missing for a year or more but returned in a later year. Forty of the absences were for 1 year, 4 for 2 years, 2 for 3 years, 2 for 4 years, and 1 for 5 years. Of 112 titmice observed in 3 or more years (thus making a skip possible), 29 (27%) skipped a year or more. This has also been reported for the Black-capped Chickadee (Elder and Zimmerman 1983) and the Great Tit (*P. major*) (Kluijver 1951).

Longevity.—The longest published record for Tufted Titmouse longevity is 13 years (Clapp et al. 1983). In my sample of 258, one bird lived to be 10 or more years old (Table 1). Although age at banding was unknown, I assumed that most birds were banded during their first winter (HY and AHY [after hatch year]). In my population, 28 birds (12%) were seen for 5 years, the same percentage that we found for the Black-capped Chickadee (Elder and Zimmerman 1983). In the large sample of titmice (N = 4460) from USFWS files, only 0.54% of recoveries exceeded 5 years

TABLE 1
MAXIMUM LONGEVITY RECORDS REPORTED FOR TUFTED TITMICE

Authority	Region	Number of birds	Oldest bird (years)
Brackbill (1970)	Maryland	130	6
Blake (1949)	Pennsylvania	Not given	7
Clapp et al. (1983)	Throughout species range	81,727	13
Condee (1969)	Pennsylvania	70	3
Laskey (1957)	Tennessee	327	6
Middleton (1969)	Pennsylvania	Not given	8[a]
Short (1933)	Michigan	5	5
Van Tyne (1948)	Michigan	29	5
This study	Missouri	258	10

[a] Cited erroneously as 12 years by Kennard (1975).

of age. Recovery data do not seem to provide a realistic estimate of survival in nonhunted species.

Influence of age.—Statistical study of changes occurring with age of my titmice revealed that (1) older birds tended to arrive at the feeder earlier in the fall than did younger birds (slope = -1.03, $r = 0.20$, N = 632, $P = 0.0001$); (2) older birds departed earlier in the spring ($r = 0.95$, N = 508, $P = 0.03$); (3) the number of times a bird was sighted did not change with age ($r = 0.026$, N = 505, $P = 0.55$); (4) the weeks a bird absented itself from the feeder did not change with age ($r = 0.014$, N = 505, $P = 0.77$); (5) the time elapsed from first capture each year until a bird was recaptured increased significantly with age (slope = 0.63, $r = 0.248$, N = 180, $P = 0.0008$); and (6) the number of times a titmouse was trapped each year was negatively correlated with age ($r = 0.114$, N = 685, $P = 0.05$).

Thus I conclude that Tufted Titmice visited the feeding station with fairly constant frequency throughout life but were trapped less frequently as they grew older and that arrival in fall and departure in spring occurred earlier with age and experience.

Survival and mortality.—A composite dynamic life table (Deevey 1947, Hickey 1952) was constructed from resighting data for all cohorts through 1979 (Table 2). From this a mean annual survival rate of 62% was calculated (Caughley 1977:105). Using equation 6a of Farner (1949) a mean life span of 2.1 years was determined—as compared to 2.4 years for our Black-capped Chickadee sample of similar size (Elder and Zimmerman 1983).

TABLE 2

LIFE TABLES FOR THE TUFTED TITMOUSE AT COLUMBIA, MISSOURI, DERIVED FROM RESIGHTING AND RETRAPPING 258 BANDED BIRDS

	Resighting data				Retrap data			
x[a]	l_x	d_x	q_x	p_x	l_x	d_x	q_x	p_x
0–1	230	94	0.41	0.59	230	163	0.71	0.29
1–2	136	34	0.25	0.75	67	31	0.46	0.54
2–3	102	47	0.46	0.54	36	16	0.44	0.56
3–4	55	20	0.36	0.63	20	8	0.40	0.60
4–5	35	16	0.46	0.54	12	3	0.25	0.75
5–6	19	6	0.32	0.68	9	5	0.56	0.45
6–7	13	6	0.46	0.54	4	2	0.50	0.50
7–8	7	0	0.00	1.00	2	1	0.50	0.50
8–9	7	6	0.86	0.14	1	1	1.00	0.00
9–10	1	1	1.00	0.00				

[a] x = age in years; l_x = survivorship to age x; d_x = number of deaths during age x; q_x = mortality during age x; p_x = survivorship during age x.

When the same procedures were used to analyze recapture data, the survival rate was lower (40%) than determined from resightings, and the mean life span was only 1.17 years. This difference would be expected because many older individuals entered the traps but avoided recapture.

Recovery data from the USFWS banding files include a total of 67,859 bandings nationwide over 60 years (1922–1981), with 4460 recoveries for a mean recovery rate of 6.5%. From a total of 60,056 bandings from 25 years (1955–1979), 1435 recoveries and recaptures have been recorded. From these data a life table was constructed and analyzed in the same way as were the Missouri data cited above. This showed a mean life span of 0.93 years and a mean annual survival rate of 0.30.

Because the numbers of recoveries were so few and inconsistent from year to year, use of the Brownie model (Brownie et al. 1979) did not prove feasible. Therefore, I constructed a table that depicts the life span shown by each banding year cohort based on recoveries and recaptures (Table 3). The rapid decline in the frequency of observations after 1960 can be accounted for mainly by the change in the reporting procedures requested by the Banding Office. Banders were no longer required to report repeats of birds recaptured at the home banding station or in the same 1-min block where banded. The effects of this change in policy are shown in Fig. 1, which depicts the very low rate of recoveries during the past two decades despite an increase in numbers of Tufted Titmice banded during the period.

When recapture and recovery data from the USFWS files were separated

TABLE 3

NUMBER OF RECOVERIES AND RECAPTURES OF 1435 TUFTED TITMICE—USFWS FILES 1955–1981

Year	Number banded	Year recovered or recaptured																								
		55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
1955	623	49	156	43	23	7	2																					
1956	1337		64	109	31	13	3																					
1957	1393			59	137	29	13	3																				
1958	1857				51	84	51	9				1																
1959	1416					38	95	15	2	1																		
1960	2722						40	59	12	3	2																	
1961	2730							11	29	2			1		1													
1962	3223								16	11	8	3	1								1	1						
1963	2426									7	8		4			1												
1964	2805										7	5	7	2		1												
1965	2650											8	11	7	2	2												
1966	2632												12	5	5	5	2	1										
1967	2910													6	7	3	5											
1968	1979														9	13	4	3										
1969	2991															7	14	2	2	1		1						
1970	3000																4	14	7	1		1						
1971	2934																	5	3	2	2	2						
1972	2913																		6	7	7	1		1				
1973	2752																			8	1	2	2	1	1			
1974	3053																				6	4	1		2			
1975	3216																					11	8	1	3			
1976	3020																						4	4	2	1	1	
1977	2456																							5	5	3	1	
1978	2632																								2	4		
1979	2895																									5	2	1
Total	60,056																											

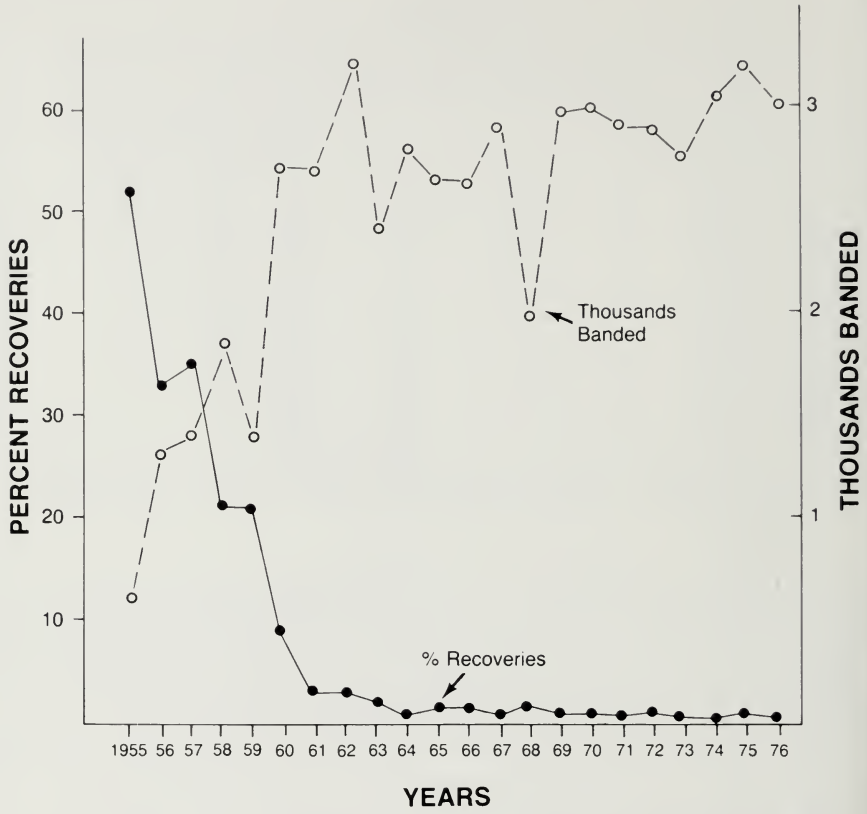

FIG. 1. Tufted Titmouse banding and recovery records from USFWS. Retrap data included only for the period available, 1955–59.

and life tables constructed for each, the calculated life span was 1.26 years for the birds recovered (dead) and 0.93 years for the birds recaptured (alive). The bias in calculating life expectancy from recaptures of live birds that have not lived out their life spans has been discussed by Hickey (1952) and Franks (1975).

The important conclusion is that careful observation and recording of a marked population of nonmigratory birds give much more realistic estimates of survival and mortality rates than does any combination of retraps and recoveries.

Movement.—Analysis of movement as shown by distance between banding station and recovery point for the 4460 birds with recovery records in the USFWS banding files showed that 40 titmice (<1%) had moved beyond the 10-min block where banded, and only 14 birds had

moved beyond 1° latitude or longitude. This clearly shows that Condee (1978) was correct in his conclusion that there is no migration in this species. The 27% of our Missouri-banded birds that were not seen for a year or more may have been only a few km away nesting or wintering.

SUMMARY

Survivorship among 258 Tufted Titmice (*Parus bicolor*) was studied by trapping, color banding, and weekly recording of sightings for 15 years at a feeder in Columbia, Missouri, from 1965 to 1979. Most birds avoided traps for a month after initial capture. Much local movement was indicated, as 80% of the December arrivals were absent in January and 67% of January arrivals were absent in February. Average residency was 18 weeks during the nonbreeding season. Individual birds were retrapped as often as 56 times, but 33% were never trapped again, even though 92% were seen after being banded. Many birds learned to avoid recapture although they fed within traps. Of birds seen in 3 or more years, 25% missed from 1 to 5 years before returning.

The oldest bird lived for at least 10 years. Older birds arrived earlier in the fall and departed earlier in the spring. They also were recaptured with decreasing frequency. Birds had a mean life span of 2.1 years and a mean annual survival rate of 62% as shown by a life table. Recapture data gave much shorter estimates than did direct observations.

Analysis of the records of the USFWS banding files showed no evidence of migration—less than 1% were recovered beyond the 10-min block where banded.

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GENERAL NOTES

Habitat and snag selection by woodpeckers in a clear-cut: an analysis using artificial snags.—When a forest is clear-cut, all trees, alive or dead, are removed. The elimination of the dead trees (snags) can have drastic effects on populations of cavity nesting birds (Webb, Trans. N. Am. Wildl. Nat. Resour. Conf. 42:438–448, 1977; Dickson et al., J. Wildl. Manage. 47:799–804, 1983). For example, woodpecker density is limited by the availability of dead or dying trees because these relatively soft substrates are required for nest and roost sites (Thomas et al., pp. 60–71 *in* Wildlife Habitats in Managed Forests, J. W. Thomas, ed., USDA For. Serv. Agric. Handbook 553, 1979). Woodpecker populations may remain low until harvested tracts provide trees of adequate size for nest cavities, usually a period of 30 or more years. Species dependent on cavities excavated by woodpeckers may, in turn, decline.

Proper forest management for wildlife requires knowledge of the habitat and nesting requirements of resident species. Probably because of their potential economic importance, woodpeckers have received much attention. Picid foraging habitat (Conner and Crawford, J. Forestry 72:564–566, 1974; Conner, J. Field Ornithol. 51:119–127, 1980), nesting habitat (Conner et al., J. Wildl. Manage. 39:144–150, 1975; Conner and Adkisson, Wilson Bull. 89:122–129, 1977), and nest-tree characteristics (Conner, Auk 92:371–374, 1975; Stauffer and Best, Wilson Bull. 94:329–337, 1982) have been well-studied. Tree hardness (Kilham, Wilson Bull. 83:159–171, 1971; Conner et al., Wilson Bull. 88:575–581, 1976), slope of branch or trunk (Conner 1975; Conner, Auk 94:369–370, 1977), and weather-related variables (Reller, Am. Midl. Nat. 88:270–290, 1972; Peterson and Grubb, J. Wildl. Manage. 47:790–798, 1983) have been considered possible causes of entrance orientation. Because of the scarcity of snags, quantification of woodpecker nesting and roosting habitat in clear-cuts is lacking.

In 1982, we initiated a study to determine if woodpeckers would excavate and subsequently roost and nest in polystyrene snags placed in an area that recently had been clear-cut. Because the artificial "trees" were homogeneous and identical in composition, selection of habitat about an excavation site could be studied under conditions free of any uncontrolled variation in the shape, size, and composition of the excavation substrate itself. The purpose of our study was to characterize patterns of woodpecker colonization of snags and orientation of cavity entrances with regard to vegetation, topography, and other snag characteristics within a clear-cut.

Study area.—Observations were made on a 3.1-ha subunit of a 12-ha, 12-year-old clear-cut in the Wayne National Forest, Hocking County, Ohio. Ridge tops in the area are characterized by oak-hickory associations. Bottomland areas are dominated by American beech (*Fagus grandifolia*), sycamore (*Platanus occidentalis*), white ash (*Fraxinus americana*), and river birch (*Betula nigra*). Our site was on a steep-terrained upland site dominated by hickories (*Carya* spp.), white oak (*Quercus alba*), red oak (*Q. rubra*), chestnut oak (*Q. prinus*), maples (*Acer* spp.), flowering dogwood (*Cornus florida*), yellow poplar (*Liriodendron tulipifera*), sourwood (*Oxydendrum arboreum*), and black tupelo (*Nyssa sylvatica*). The clear-cut was densely vegetated, averaging 9250 trees/ha. Canopy height averaged approximately 8 m. The northwest and southeast sides of our plot were bordered by extensions of the clear-cut, the southwest side by a mature forest, and the northeast side by a road bordered by a forested tract (Petit, M.S. thesis, The Ohio State Univ., Columbus, Ohio, 1984). An ephemeral creek flowed southwest through the site and was bordered on both sides by relatively steep slopes. Elevation within the plot ranged from 240 to 275 m. There was little fallen or standing dead timber on the clear-cut.

Methods.—On 4 September, we placed 99 polystyrene snags, each measuring 237 × 21 × 21 cm, in the clear-cut. These dimensions are within or very near to the range of sizes of snags used by six species of woodpeckers that are found in Ohio during most of the year (Conner, pp. 120–128 *in* Management of Southern Forests for Nongame Birds, R. M. DeGraaf, tech. coord., USDA For. Serv. Gen. Tech. Rept. SE-14, 1978; Evans and Conner, pp. 214–225 *in* Management of North Central and Northeastern Forests for Nongame Birds, R. M. DeGraaf and K. E. Evans, eds., USDA For. Serv. Gen. Tech. Rept. NC-51, 1979). Although the height and diameter of the artificial snags may have been acceptable to Red-bellied Woodpeckers (*Melanerpes carolinus*), Northern Flickers (*Colaptes auratus*), Red-headed Woodpeckers (*M. erythrocephalus*), and Yellow-bellied Sapsuckers (*Sphyrapicus varius*), they were most suitable for Downy Woodpeckers (*Picoides pubescens*) and Hairy Woodpeckers (*P. villosus*). A hole was drilled lengthwise approximately 80 cm into the base of each polystyrene snag. Each snag was then painted with brown latex paint and fixed atop a 1.5-m fiberglass stake driven approximately 75 cm into the ground. Snags were positioned to face only the four cardinal directions. Because of the steep terrain and soil creep over the course of the study period, some of the artificial snags came to lean up to 20° from the vertical. The 99 snags, spaced 16 m apart, were arranged in an 11 × 9 grid pattern, and were examined at approximately biweekly intervals during the following 12 months for evidence of excavating activity by woodpeckers. A cavity was defined as an excavation at least 10 cm deep on the vertical axis from the lower lip of the entrance hole (Grubb, Wilson Bull. 94:577–579, 1982). To determine the effects of vegetation, topographical, and snag features on woodpecker cavity-site selection, we recorded 32 variables within 0.02-ha (8-m radius) circles centered on each of the snags (Table 1).

Differences between polystyrene snags with cavities and those without cavities were analyzed by using both univariate and multivariate statistical methods. Values for all variables were first tested for departure from a normal distribution (Shapiro-Wilks test; SAS User's Guide: Basics, SAS Institute, Cary, North Carolina, 1982). If nonnormal, a given variable was transformed appropriately (Steel and Torrie, Principles and Procedures of Statistics, McGraw-Hill Book Co., New York, New York, 1980). All normalized variables were tested for differences between groups by a one-way analysis of variance (ANOVA). Those variables that could not be fitted to a normal distribution were tested with the Mann-Whitney *U*-test.

Multivariate ordination techniques reduce the number of variables to one or more functions that best describe the variability within a sample set (see Morrison, Multivariate Statistical Methods, McGraw-Hill Book Co., New York, New York, 1976; Gauch, Multivariate Analysis in Community Ecology, Cambridge Univ. Press, New York, New York, 1982). Stepwise discriminant function analysis (DFA; Dixon and Brown, BMDP Biomedical Computer Programs P-series, Univ. California Press, Berkeley, California, 1979) determines those variables that best separate two or more groups (e.g., James, Wilson Bull. 83:215–236, 1971; Conner et al., Wilson Bull. 95:349–361, 1983). In our study, DFA combined the habitat variables into the discriminant function that most effectively segregated snags with cavities from those without cavities. Because the number of variables entered into the stepwise DFA must be less than the smallest sample size, we reduced the number of variables entered into the DFA. This also minimized the effect of relatively unimportant variables (Nie et al., Statistical Package for the Social Sciences, McGraw-Hill Book Co., New York, New York, 1975). Those variables that exhibited a difference of $P < 0.15$ by ANOVA or *U*-tests and that did not differ greatly from the statistical assumptions were selected for the multivariate analysis.

A chi-square test was used to test for randomness in cavity entrance orientation. For statistical analyses, alpha levels ≤ 0.05 were taken as indicating significant differences.

We placed our 11 × 9 grid of polystyrene snags in the clear-cut so that 13 snags extended

Table 1

Vegetation, Topographic, and Polystyrene Snag Characteristics Measured within 0.02-ha Circular Plots around the 99 Artificial Snags Erected in a Clear-Cut in Southeastern Ohio

Variable mnemonic	Description
CANCOV[a]	Percent canopy cover: the number of sightings of canopy vegetation at 20 points within the circle.
CANHT	Canopy height (m)
CCANCOV[a]	Percent coniferous canopy cover: the number of sightings of coniferous canopy vegetation at 20 points within the circle.
GRDCOV[a]	Percent ground cover: the number of sightings of ground cover (<0.6 m tall) at 20 points within the circle.
SLOPE[b]	Ground slope: a value measured at a representative point within the circle.
DISTOPEN	Distance (m) to nearest opening >100 m^2 in size.
DISTWOOD	Distance (m) to nearest mature woodland.
TREESA	Number of woody plants ≤1.0 cm DBH.
TREESB	Number of woody plants 1.1–2.5 cm DBH.
TREESC	Number of trees 2.6–8.0 cm DBH.
TREESD	Number of trees 8.1–15.0 cm DBH.
TREESE	Number of trees 15.1–23.0 cm DBH.
TREESX	Number of trees >23.0 cm DBH.
CTREESA	Number of coniferous trees ≤1.0 cm DBH.
CTREESB	Number of coniferous trees 1.1–2.5 cm DBH.
CTREESC	Number of coniferous trees 2.6–8.0 cm DBH.
CTREESD	Number of coniferous trees 8.1–15.0 cm DBH.
CTREESE	Number of coniferous trees >15.0 cm DBH.
SPTREES	Number of species of woody plants.
TOTTREES	Total number of woody plants ≥1.4 m high.
TOTCTREES	Total number of coniferous trees ≥1.4 m high.
SNAGBC	Number of snags 1.1–8.0 cm DBH.
SNAGDE	Number of snags 8.1–15.0 cm DBH.
SNAGX	Number of snags >15.0 cm DBH.
NEARTRA	Number of woody plants ≤1.0 cm DBH within a 1-m radius of a polystyrene snag.
NEARTRB	Number of woody plants 1.1–2.5 cm DBH within a 1-m radius of a polystyrene snag.
NEARTRC	Number of trees 2.6–8.0 cm DBH within a 1-m radius of a polystyrene snag.
NEARTRD	Number of trees 8.1–15.0 cm DBH within a 1-m radius of a polystyrene snag.
NEARTRE	Number of trees 15.1–23.0 cm DBH within a 1-m radius of a polystyrene snag.
NEARTRX	Number of trees >23.0 cm DBH within a 1-m radius of a polystyrene snag.
TRSLOPE	Polystyrene snag lean: the number of degrees that snag alignment departed from the vertical, estimated to the nearest 5°.
TRASPECT	Aspect of polystyrene snag lean: measured as one of the four cardinal directions.

[a] See James and Shugart (Audubon Field Notes 24:727–736, 1970).
[b] Measured with an instrument similar to that of Fovargue and Perino (Ohio J. Sci. 79:130–132, 1979).

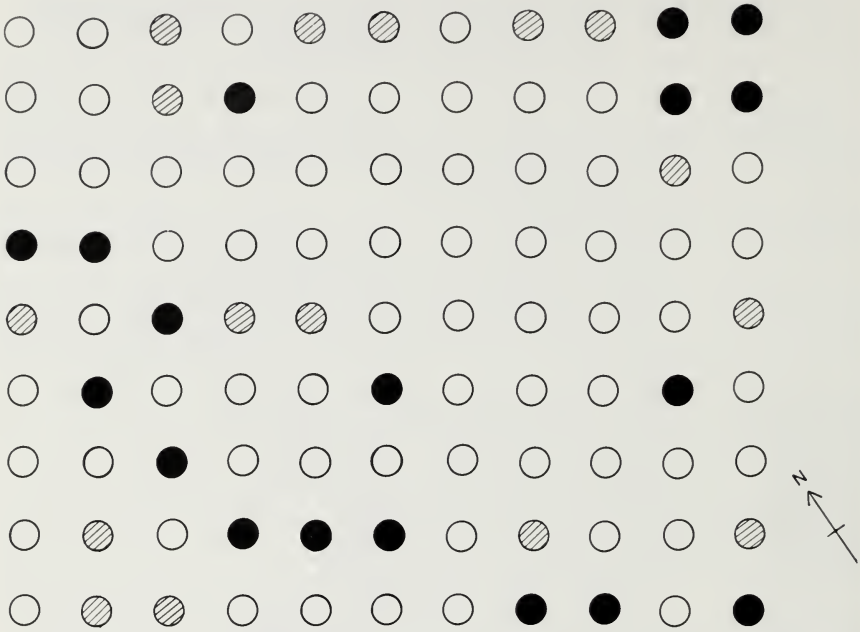

FIG. 1. Sequence of cavity excavations in the artificial snags on the clear-cut in southeastern Ohio. Cross-hatched circles represent snags excavated from October to March. Shaded circles are those snags excavated from April to September.

into the mature woodland on the southwest border. This enabled us to assess the presence of woodpeckers in an adjacent mature tract and determine if they tended to avoid the clear-cut or if there was an avoidance of the square-sided snags in general. Because of the differences in vegetation between these two areas and because there might have been seasonal or serial correlation with the choice of snag attributes, the univariate and multivariate methods for determining snag-habitat selection were repeated for four pairs of comparisons. The analyses contrasted the habitats surrounding snags with cavities (CAVITY) against the habitats around snags without cavities (NOCAVITY) for (1) snags in the clear-cut proper from October to March (CCWINTER), (2) snags in the entire plot from October to March (TOTWINTER), (3) snags in the clear-cut proper from October to September (CCYEAR), and (4) snags in the entire plot from October to September (TOTYEAR).

Woodpecker abundances.—During the 18 months after placing the polystyrene snags in the clear-cut, we conducted 40, 43, and 7 line-transect censuses in the clear-cut, and the mature woodlands on the northeast and southwest sides of the clear-cut, respectively (Petit, unpubl.). Here, we summarize briefly the relative abundances of woodpeckers. In the clear-cut, Downy and Hairy woodpeckers were detected in 20% and 10% of the censuses, respectively. No other species of woodpecker was counted within the clear-cut. In the mature woodlands, flickers (in up to 29% of the censuses), Pileated (*Dryocopus pileatus*) (up to 14%), Red-bellied (up to 29%), and Hairy (up to 40%) woodpeckers were detected regularly. In the plot on the northeast side of the clear-cut, Downy Woodpeckers were present in 49% of the censuses, but in the southwest woodland, downies were never seen during our seven

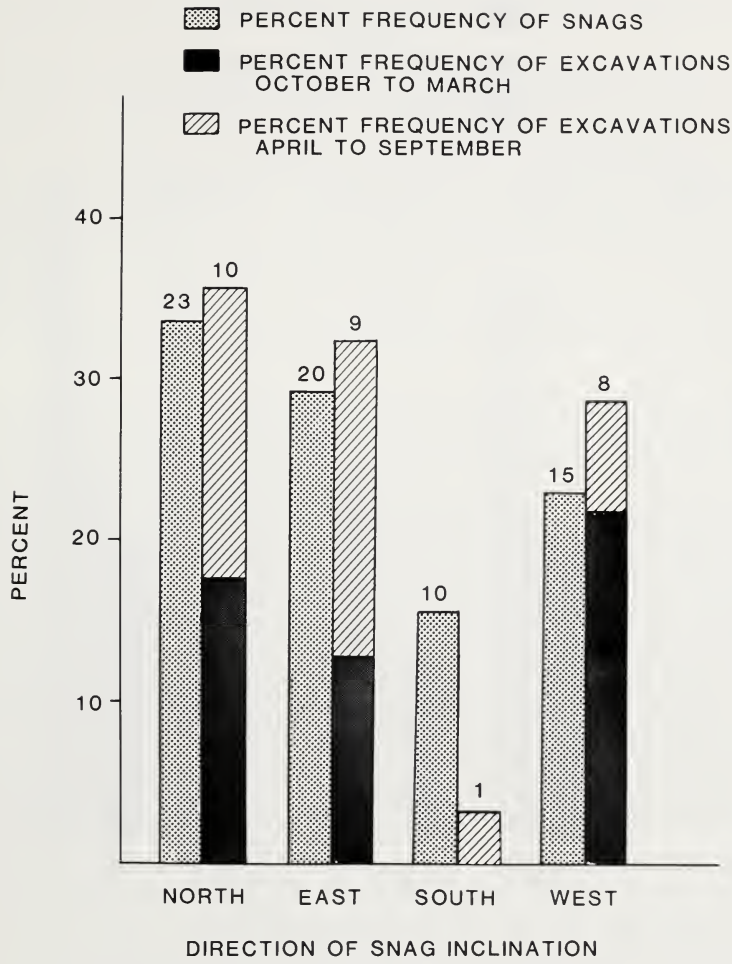

FIG. 2. The relationship between the expected use of the 68 leaning snags and the observed pattern of 28 excavations. The values above the histograms represent the number of leaning snags or the number of excavations for a given direction of snag inclination.

counts. It appears that the larger woodpeckers avoided the clear-cut altogether, and Downy and Hairy woodpeckers were less common there as compared to the surrounding mature forest. Because of these observations, our nighttime observations (see below), and the cavity entrance characteristics (see below), we believe that the woodpecker species using our artificial snags probably was the Downy Woodpecker.

Cavity entrance orientation.—The first full cavity was discovered during early October 1982, 4 weeks after the snags were placed in the clear-cut; and by 1 April 1983, 16 cavities had been dug (Fig. 1). In all instances (15 of 16) in which the snag was not exactly vertical, the entrance was on the "underside" of the snag. Snags were examined at night once in

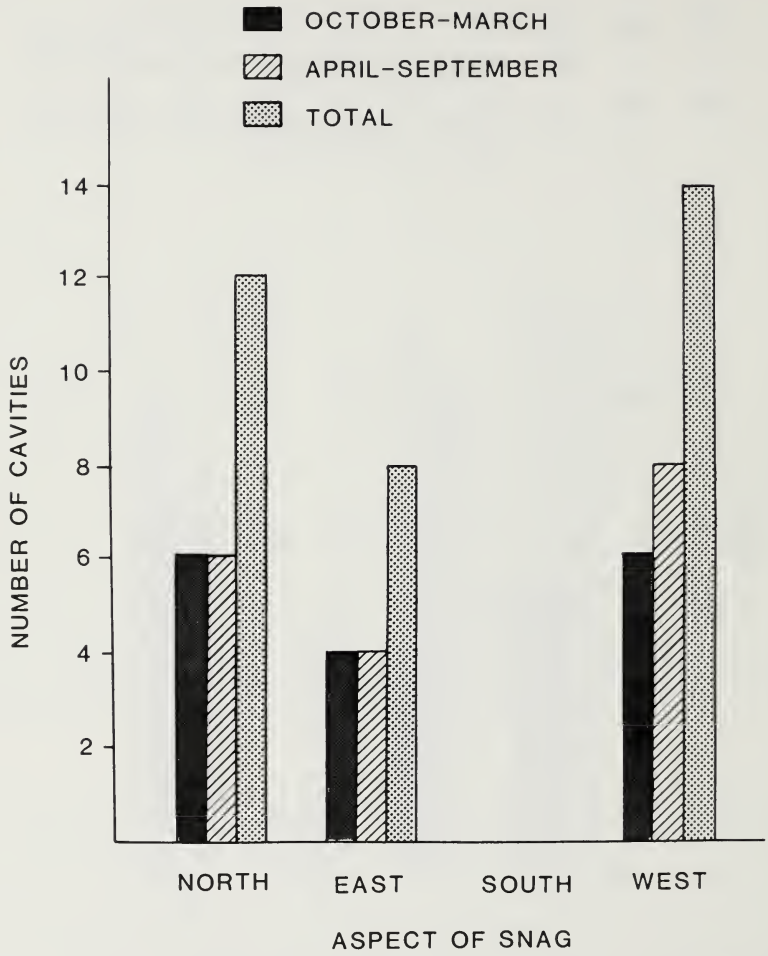

FIG. 3. Frequency of cavity entrance placement on each of the four aspects of the 34 excavated artificial snags.

December and once in February. On both evenings, two Downy Woodpeckers were found roosting in different snags.

Eighteen additional cavities were excavated from April to September (Fig. 1). Thirteen of the 18 excavated snags were nonvertical, and nine of these 13 had cavity entrances placed on the underside. A chi-square test for goodness-of-fit confirmed the relationship between direction of snag lean and cavity orientation ($P > 0.40$). To ascertain whether woodpeckers were selecting leaning snags regardless of the direction of the inclination of the snag, we calculated the proportion of the 68 leaning snags that slanted in each of the four cardinal directions and compared these proportions to the frequencies with which each of the four categories was used (Fig. 2). Woodpeckers did not excavate the inclining snags in the pro-

TABLE 2

MEAN ± SD OF CAVITY AND NOCAVITY SNAG CHARACTERISTICS SHOWING SIGNIFICANT ($P < 0.05$) DIFFERENCES FROM OCTOBER TO MARCH

Variable	Clear-cut		Entire plot	
	Snags with cavities (N = 13)	Snags without cavities (N = 73)	Snags with cavities (N = 16)	Snags without cavities (N = 83)
CANCOV	88.5 ± 9.7	94.7 ± 4.2	88.8 ± 8.9	94.4 ± 4.6
DISTOPEN	35.9 ± 28.0	55.9 ± 30.9	—	—
CTREESA	0.3 ± 0.5	0.1 ± 0.2	—	—
TRSLOPE	8.8 ± 6.2	4.9 ± 4.4	8.4 ± 5.7	4.7 ± 4.4

portions present ($P < 0.05$); they rarely excavated snags that leaned toward the south. Similarly, of the 34 snags that contained cavities, none had a completed excavation on the south-facing side ($P < 0.05$, chi-square test of randomness; Fig. 3). Cavity entrance orientation did not vary seasonally (Fig. 3).

Wind and solar radiation affect the direction toward which cavity nesters orient their entrances (Ricklefs and Hainsworth, Ecology 49:227–233, 1968; Austin, Condor 76:216–217, 1974). Conner (1975) and Peterson and Grubb (1983) concluded that, in their study areas, orientation away from the prevailing wind direction prevented rain and cold air from entering the cavity. In southeastern Ohio, the predominant wind direction is from the southwest. The placement of cavity entrances in our study on the west side of snags, but not on the south side, is, therefore, difficult to interpret. Possibly, the south-facing side was more exposed to the prevailing wind than was the west-facing side because of the orientation of the valley in which the snags were situated. This valley is oriented from NNE to SSW. Wind might be funnelled up through the valley, and, therefore, might have caused the south side of the polystyrene snags to be the most susceptible to weather effects. Our results support the suggestion that tree lean is the most important factor governing woodpecker cavity entrance orientation (Conner 1975).

Cavity characteristics.—Cavity entrance area (15.1 ± 3.3 [SD] cm^2) and distance from the cylinder's top to the center of the entrance hole (45.8 ± 30.5 cm) did not vary greatly among the 34 cavities. "Summer" and "winter" cavities did not differ significantly in either of these characteristics (Petit 1984). Peterson and Grubb (1983) observed that during the warmer months woodpeckers dug larger entrances, which were thought to increase the ventilation of the cavity. The cavities excavated after March in this study, however, did not appear to receive much use (i.e., they were not soiled). More than three-fourths of the cavities were dug in the upper quarter of snags. Such higher cavities might be less noticeable and less accessible to predators.

The entrance dimensions of all but three of the 34 cavities suggest that they were dug by Downy Woodpeckers. Three snags in close mutual proximity within the band of large trees near the southwest border of the clear-cut had cavity entrances much larger than those of any other cavity (21.9, 24.0, and 25.5 cm^2). All three cavity entrances were wider than high. Northern Flickers, Red-bellied Woodpeckers, and Hairy Woodpeckers were seen foraging near these snags, and an individual or individuals of one of these species was likely the excavator.

Cavity site selection.—Snags excavated from October to March (CCWINTER; N = 13) in the clear-cut proper were not selected randomly. CAVITY snags were characterized by lower

TABLE 3

MEAN ± SD OF CAVITY AND NOCAVITY SNAG CHARACTERISTICS SHOWING SIGNIFICANT ($P < 0.05$) DIFFERENCES FROM OCTOBER TO SEPTEMBER

Variable	Clear-cut		Entire plot	
	Snags with cavities (N = 27)	Snags without cavities (N = 59)	Snags with cavities (N = 34)	Snags without cavities (N = 65)
CANCOV	91.7 ± 7.9	94.7 ± 4.3	—	—
TREESB	41.0 ± 17.2	51.3 ± 21.8	36.1 ± 18.0	49.2 ± 22.4
NEARTRC	1.2 ± 1.4	1.7 ± 1.5	0.9 ± 1.3	1.5 ± 1.5
TRSLOPE	7.1 ± 6.0	4.8 ± 4.2	6.6 ± 5.6	4.6 ± 4.2
TREESC	—	—	59.9 ± 31.1	72.6 ± 27.4
TOTTREES	—	—	153.3 ± 58.8	183.3 ± 53.8

canopy cover and distance to an opening, higher numbers of small coniferous trees, and a greater degree of inclination of the snags (Table 2). Three variables contributed significantly to the separation of the group centroids (DFA; $F = 12.5$; $df = 3,82$; $P < 0.001$). The single discriminant function is positively correlated with snag inclination and negatively correlated with percent canopy cover and distance to an opening. Thus, woodpeckers concentrated their excavating activities on inclining snags in areas of relatively sparse canopy cover close to an opening around or within the clear-cut. The ability of the discriminating variables to separate the two groups was tested empirically by a classification technique, i.e., comparing predicted group membership based only upon the discriminating variables with the observed group membership (see Nie et al. 1975). For CCWINTER, the DF correctly classified 80.2% of the artificial snags, demonstrating a high degree of cavity site selection by woodpeckers during the first six months.

The TOTWINTER comparison yielded similar results. The only two variables to show significant differences in the univariate tests (Table 2), also comprised the DF. Canopy cover and snag inclination significantly segregated group centroids ($F = 13.3$; $df = 2,96$; $P < 0.005$) and, as with CCWINTER, were negatively and positively associated with the DF, respectively. Snags with cavities were generally situated along the portion of the DF axis associated with low canopy cover and high snag lean. A high degree of snag selection by woodpeckers was indicated by the correct classification of 74.7% of the polystyrene snags.

Throughout the year, 27 cavities were excavated within the clear-cut. General univariate patterns showed reduced canopy cover, small trees (TREESB), and nearby trees of 2.6–8.0 cm DBH for CAVITY snags. Polystyrene snags with cavities leaned more than snags that had not been excavated (Table 3); however, only the nearby trees of 2.6–8.0 cm DBH had sufficient discriminating ability to be included in the DF model. Although this single-variable discriminant axis significantly distinguished between group centroids for the CCYEAR analysis ($F = 5.5$; $df = 1,84$; $P < 0.025$), group membership was predicted correctly for only 54.7% of the snags.

On the entire plot throughout the year, 34 cavities were excavated. Five habitat variables were significantly different between CAVITY and NOCAVITY snags. There were more trees of 1.1–8.0 cm DBH, more total trees, and more nearby trees of diameter 2.6–8.0 cm around snags lacking cavities, while snags with cavities leaned to a greater degree (Table 3). Group means differed significantly along the DF axis ($F = 6.1$; $df = 2,96$; $P < 0.01$), which was positively correlated with snag lean and negatively associated with nearby trees of 2.6–8.0

cm DBH. Although group distributions overlapped moderately, 67.7% of the artificial snags were correctly categorized.

Several patterns of habitat selection by cavity-excavating Downy Woodpeckers are indicated by the above analyses. First, during the autumn and winter, canopy cover was the most important habitat variable in snag selection. On at least five occasions, we saw woodpeckers (downy, red-bellied, pileated, and flickers) flying over the clear-cut from the forest on the northeast side to the woodland on the southwest border of the clear-cut. Leaves remained on the trees until late October, so the initial use of the clear-cut might have been enhanced by the reduced canopy cover around some of the snags. This might have provided woodpeckers with less obstructed access to some of the snags. Also, some of the snags might have been visible to the woodpeckers flying over the otherwise dense canopy of the clear-cut. Once Downy Woodpeckers began using these cavities as roost-sites, other snags with greater canopy cover could have been discovered during foraging movements within the clear-cut. Distance to an opening was a function of the distance to the clear-cut borders. During the "winter" period, 81.3% (13 of 16) of the snags selected were within 35 m of the clear-cut edge. Likewise, 76.5% (26 of 34) of the total snags excavated exhibited this nonrandom pattern. By selecting roost sites near the edge, woodpeckers could have been retaining ready access to more than one habitat type (Strelke and Dickson, J. Wildl. Manage. 44:559–567, 1983).

Woodpeckers favored snags placed in mature woodland, as they excavated 54% (7 of 13) of the snags placed in the band of large trees on the southwest margin of the clear-cut as compared to 31% (27 of 86) of the snags within the clear-cut. This result arose because woodpeckers prefer mature stands. Peterson and Grubb (1983) found that Downy Woodpeckers dug cavities in 84% of the artificial snags they placed in a mature bottomland woodlot.

The lack of trees 2.6–8.0 cm DBH (NEARTRC) close to snags with cavities might reflect an antipredator strategy. Medium-sized mammalian predators apparently had difficulty climbing the polystyrene snags (e.g., claw marks indicated that the polystyrene could not usually support a predator's weight as it climbed the snag), so a nearby tree could have provided the means by which such a mammal could have seized a roosting bird or nest-cavity contents. Trees smaller than 2.5 cm DBH probably cannot support a raccoon (*Procyon lotor*) or opossum (*Didelphis virginiana*). Trees greater than 8.0 cm DBH also were scarcer around CAVITY snags.

Our results indicate that snags used for management purposes should be placed in relatively open patches within the clear-cut. Also, at least some of the snags should be placed near the edges of the clear-cut. This placement might accelerate woodpecker colonization by providing the woodpeckers with greater visibility and access to the introduced snags. Finally, the polystyrene snags should be placed so that they lean slightly and a small area should be cleared around them.

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Differences in the feeding behavior of Little Egrets (*Egretta garzetta*) in two habitats in the Camargue, France.—Relationships among predators, prey, and the habitats they use are of continued interest in behavioral ecology. Holling (Can. J. Entomol. 91:293–320, 1959) distinguished between two types of predator responses to changes in prey abundance: numerical and functional. The first response occurs at the population level, and the second at the individual level. Studies of the functional response were pioneered by Gibb (Ibis 102: 163–208, 1960), L. Tinbergen (Arch. Neerl. de Zool. 13:265–336, 1960), Royama (J. Anim. Ecol. 39:619–669, 1970; Proc. Adv. Study Inst. Dynamics Numbers Popul. [Oosterbeek]: 344–357, 1970), and others on foraging theory, and their studies have become the stage upon which optimal foraging theory has developed.

Recently, a number of studies have related prey density and distribution to predator behavior (e.g., J. Tinbergen [Ardea 69:1–67, 1981], Goss-Custard [J. Anim. Ecol. 39:91–113, 1970; J. Anim. Ecol. 46:867–874, 1977], and Pienkowski [Anim. Behav. 31:244–264, 1983; Mar. Ecol. Prog. Ser. 11:141–150, 1983]). In the Camargue, southern France, extensive work is being conducted on prey densities and the feeding behavior of Little Egrets (*Egretta garzetta*) (Hafner, Terre et Vie 32:279–289, 1978; Hafner et al., Ardea 70:45–54, 1982; Hafner and Britton, Colonial Waterbirds 6:24–31, 1983). This study is part of that work. Here we (1) compare prey type and abundance and feeding behavior of birds at two different habitats, an artificial shallow marsh and a natural freshwater marsh; (2) compare feeding behavior of birds using different microhabitats; and (3) determine how extrinsic factors such as group size, time of day, and reduced water levels influence feeding behavior.

Study area and methods.—The study was conducted in July 1984 on the Tour du Valat, a former 1900-ha farm located in the arid hypersaline eastern region of the Camargue Regional Park in the Rhone River delta. The Camargue includes an area of ca. 85,000 ha in Mediterranean France and is noted for its dry, windy climate and its mosaic of wetlands that include both temporary and permanent marshes (ranging from freshwater to hypersaline), and extensive active and abandoned rice fields with interconnecting canals.

We used observation hides at two sites to watch feeding egrets that nested in the vicinity. St. Seren is a large natural, freshwater marsh that provides important feeding and roosting habitat for wading birds during the nesting season (April through July) and for waterfowl in winter. A large permanent hide constructed at the south end of the marsh has been used for a number of years to census aquatic birds (Station Biologique de la Tour du Valat, unpubl. reports). This hide served as one of our observation points. The portion of the marsh that could be observed from our hide ($\geq$4 ha) was classified into three microhabitat types: open water (predominant), edges ($\leq$1 m) of *Scirpus* spp. patches, and interior portions of *Scirpus* patches. St. Seren was subject to continuous drying during the observation period and was completely dry by 19 July.

The other site, field C13, is an artificial shallow marsh, one of a series of interconnected marshes whose water levels are maintained during the summer. This 1-ha field was composed of a relatively uniform cover of grasses and sedges ca. 15–30 cm in height. Water levels remained at about 10–15 cm during July. Such marshes become important feeding sites for wading birds as natural marshes dry up (Hafner 1978). This marsh and several adjacent ones had been used by egrets throughout the nesting period; therefore a 3.5 m high hide had been erected adjacent to C13 in June. The two sites were selected to represent the two most important feeding habitat types for wading birds in the eastern Camargue (Hafner 1978, Hafner et al. 1982).

Observations of feeding birds were conducted between 3 and 26 July 1984. A prey sampling

TABLE 1

PREY ABUNDANCE[a] FOR THROW-TRAP SAMPLES AT ST. SEREN AND C13 MARSHES

Prey	No. of prey items per sample	
	St. Seren	C13
Fish	1.0 ± 1.5	0
Tadpoles	0	7.9 ± 6.8
Hydrous piceus	0.3 ± 0.6	3.3 ± 2.7
Other invertebrates	61.1 ± 21.6	16.6 ± 10.1
Total prey	62.4 ± 21.4	27.8 ± 15.0

[a] Means ±1 SE for St. Seren (N = 21) and C13 (N = 15) samples taken 2 July and 12 July, respectively.

scheme was devised using one-m^2 throw traps (Kushlan, Trans. Am. Fish. Soc. 103:348–352, 1974). Fifteen samples were taken from field C13 on 12 July, and 21 samples were taken at St. Seren on 2 July. Samples were taken 5–10 m apart along a randomly selected transect line at each site. Earthwatch participants (Earthwatch is a Massachusetts-based nonprofit conservation organization that supports scientific field research through the use of lay volunteers who provide their time and financial support) conducted the sampling using hand sieves to collect potential prey organisms in the water column and the top 0.5–1.0 cm of bottom sediments within the one-m^2 trap perimeter. Hand sieving continued until three consecutive sweeps produced no organisms. Prey were removed with forceps and placed in labelled glass vials containing alcohol. They were later identified (to family or genus usually), counted, and measured in the laboratory.

Feeding egrets were watched with binoculars and spotting scopes from the hides. Data were collected continuously using cassette tape recorders and blocked into 5-sec increments on standard forms. Observation periods lasted from 30 min to 3 h, depending on numbers of birds using a site. Our goal was to observe at least 5 individuals for at least 5 min each during each observation period. The following data were collected: date, time, and numbers of feeding birds seen upon our arrival; feeding rates (FR, the number of pecks per min), success rate (SR, the number of captures per min), efficiency (EF, or SR/FR), movement rate (MR, the number of steps per min), turning rate (TR, the number of changes in direction [N, E, S, W] per min while feeding), and stirring rate (STR, the number of foot-stirs per min). We also recorded the number of other feeding birds within 5 m of the focal individual each min. Focal individuals were chosen haphazardly and, whenever possible, followed for a minimum of 5 min during a feeding bout. Notes were taken of agonistic interactions. At St. Seren, the microhabitat of the feeding individual was recorded each minute as either open water, *Scirpus* patch, or edge of patch. Eight feeding areas of different sizes were designated on a map using microhabitat features as landmarks. These areas were denoted to monitor spatial and temporal changes of feeding birds and to monitor indirectly changes in water levels. Water level readings could not be measured directly for logistical reasons. Identification of prey items taken by egrets was usually not possible because of the small size of the prey (except for relatively large water beetle [*Hydrous piceus*] larvae, which were frequently 6–7 cm long).

We conducted *t*-tests and least squares regression analyses using the Statistical Analysis System (Helwig and Council, eds., SAS User's Guide—1979 edition, SAS Institute, Cary, North Carolina, 1979). For most of the analyses, the individual bird was the sampling unit;

TABLE 2
COMPARISON OF FEEDING BEHAVIOR OF LITTLE EGRETS AT ST. SEREN MARSH WITH THAT AT C13

Behavior	Site	
	St. Seren (N = 50)	C13 (N = 29)
Pecks/min	5.4 ± 0.8[a]	2.1 ± 0.2
Captures/min	3.2 ± 0.5	1.5 ± 0.1
Changes in direction/min	2.6 ± 0.3	1.3 ± 0.1
Foot-stirs/min	5.2 ± 0.8	0.3 ± 0.1

[a] Means ± SE of the individual mean scores; morning periods only.

therefore, means were generated for feeding variables based on observations of from 2 to 16 min.

Prey populations.—The two sites had similar prey species except that at St. Seren no frog tadpoles were found, and at C13 no fish (mosquito fish [*Gambusia affinis*] and sticklebacks [*Gasterosteus* spp.]) were present in any samples. Important invertebrate prey that were common in the samples were large (5–8 cm) water beetle larvae, backswimmers (*Notonecta* spp.), odonate nymphs, *Corixa* spp., *Naucoris* spp., and various beetle larvae. Most prey items (except *Hydrous*) were <2 cm long.

Significant differences in the relative numbers of individual prey were found between the two sites (*t*-tests, df = 34, all $P < 0.01$) (Table 1). Individual prey densities per sample were more than twice as great at St. Seren as at C13. Although mean prey densities were lower at C13 than at St. Seren, the among-sample variation at C13 was greater (Coefficient of Variation [CV] = 54% at C13; CV = 34% at St. Seren). Thus, C13 was patchier in its total prey distribution than the natural marsh.

Feeding behavior.—Because St. Seren dried up during the observation period, we examined the possibility that temporal changes in prey density caused by reduced water area affected heron feeding behavior. Least squares regression analyses were conducted for each feeding variable from 7 July (when all 8 zones had water) to 16 July (when only 1 had water). There was no significant trend ($P > 0.05$) for any variable except turning rate, which decreased over the 9-day period ($t = -2.98$, df = 1, 36, $P < 0.01$). Also, there was no strong numerical response by the birds as might be expected if prey became more concentrated (Kushlan et al., U.S. Geol. Surv. Open File Rept. No. 75–434, 1975). Numbers fluctuated daily from 8 to 29 during the morning periods ($\bar{x} = 16$, CV = 44%) and from 12 to 63 in the afternoons ($\bar{x} = 28$, CV = 72%), with no significant linear trend ($P > 0.05$).

The effect of time of day was examined only at the C13 site because few data were collected at St. Seren in the afternoon. At C13, 4 morning periods (29 birds) were compared to 6 afternoon periods (32 birds). Morning feeding rates were significantly greater ($\bar{x} = 2.4 \pm 0.2$) than afternoon rates ($\bar{x} = 1.8 \pm 0.1$; $F = 4.01$, df = 1, $P < 0.05$). Similarly, foot-stirring was more frequent in the morning ($\bar{x} = 0.4 \pm 0.1$) than the afternoon ($\bar{x} = 0.1 \pm 0$; $F = 5.77$, df = 1, $P < 0.02$). The other variables showed no significant differences ($P > 0.05$).

To examine whether microhabitat differences influence feeding behavior, we compared the behavior of birds feeding in open water (N = 30), on the edge (N = 12), and in patch interiors (N = 19) at St. Seren. Data were pooled over all days. Birds moved faster in open water than in the other two microhabitats ($F = 11.3$, df = 2, $P < 0.01$ and Duncan's MR

TABLE 3

RELATIONSHIP BETWEEN GROUP SIZE[a] AND FEEDING BEHAVIOR OF LITTLE EGRETS

Behavior	Group size[b]		
	Solitary (N = 31)	Few (N = 32)	Many[c] (N = 43)
Pecks/min	2.62 ± 0.34	2.31 ± 0.31	4.93 ± 0.81[CD]
Captures/min	1.80 ± 0.24	1.54 ± 0.21	3.07 ± 0.58[CD]
Captures/peck	0.76 ± 0.05	0.67 ± 0.04	0.59 ± 0.03[C]
Steps/min	15.01 ± 1.87	16.91 ± 1.60	25.42 ± 1.78[CD]
Changes in direction/min	1.27 ± 0.16	1.35 ± 0.21	2.47 ± 0.30[CD]
Foot-stirs/min	1.92 ± 0.90	1.53 ± 0.60	3.69 ± 0.81

[a] Group size based on average no. of birds within 5 m of focal bird; see text for size definitions.
[b] Means ± SE given.
[c] Results of Duncan's and Scheffe's MR tests shown. A "C" indicates a significant difference ($P < 0.05$) between column 3 and column 1 values; a "CD" indicates that column 3 value is significantly different from both column 1 and column 2 values.

test); however, the other four variables (FR, SR, TR, STR) did not vary significantly with microhabitat ($P > 0.05$).

To compare sites, we pooled the St. Seren sample, excluding the movement rate data that showed microhabitat variation. Because of the influence of time of day (above), we compared only morning observations. Nearly a twofold difference in rates was found between sites (Table 2).

Little Egrets feed in a variety of social contexts, ranging from territorial (solitary) feeding to large groups (Hafner et al. 1982, P. Dugan, unpubl. data). We recognized three group-size classes of neighboring feeding birds, based on the average number of "neighbors" (within 5 m) observed at the beginning of each 1-min sample period. Birds were classified into solitary, "few" (mean >0, <2.0), and "many" (mean >2.0). For FR, SR, MR, and TR, birds with "many" neighbors had higher rates than solitary feeders or those with "few" neighbors (Table 3). Efficiency was higher for solitary birds than for those in larger groups.

Discussion.—A twofold difference in overall prey density at the two sites was mirrored in nearly twofold differences in feeding, success, and turning rates and even larger differences in stirring rates. Caution must be exercised, however, in directly relating prey *densities* to feeding behavior. The sites also differed in microhabitats. St. Seren was primarily open water with mud bottom, while the rice field had a relatively uniform grass-sedge cover. Thus, prey *availability,* in addition to density, may also contribute to differences in feeding behavior.

The results found in this study concerning movement rates are opposite to those reported by Hafner et al. (1982) in the same region. Whereas the egrets we watched moved nearly twice as rapidly in St. Seren as in C13, Hafner et al. (1982) found that movement was greater in rice fields than marshes. The rice fields studied by Hafner et al. were different enough from our artificial marsh that a direct comparison is probably not justifiable.

The influence of other birds feeding nearby resulted in major differences in feeding behavior. In general, egrets in large (>2) groups were much more active than those feeding alone or in pairs. This difference may reflect local enhancement, i.e., an aggregation of birds at localized sites after one or two birds discover a "hot spot," begin feeding rapidly, and in turn attract others. We noted this behavior on several occasions at St. Seren. Hafner et al.

(1982) found that the percentage of successful pecks in flocks of birds was greater than for solitary birds; however, our results showed that solitary birds were more efficient than those in larger groups. This effect could be caused by direct interference in larger groups, or by a change in prey behavior with increases in the number of predators (K. Bildstein, pers. comm.).

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Interactions between Great Blue Herons and gulls.—Previous reports of interactions between Great Blue Herons (*Ardea herodias*) or Gray Herons (*A. cinerea*) and gulls (*Larus* spp.) have been largely anecdotal, and they indicate that the interactions are generally immediately selfish. For instance, interactions have included food piracy (Lowe, The Heron, Collins, London, England, 1954; Dummigan, Br. Birds 70:117, 1977; Willard, Condor 79: 462–470, 1977; Quinney et al., Can. Field-Nat. 95:205–206, 1981), mutual cueing to each other's feeding flocks (Marshall, Br. Birds 54:202, 1961), or gulls mobbing predatory Gray Herons in gull colonies (Axell, Br. Birds 49:193–212, 1956). There have, however, also been several accounts of gulls attacking Great Blue Herons (Imhof, Wilson Bull. 62:210, 1950) or Gray Herons (Lowe 1954:109–110; Birkhead, Br. Birds 66:147–156, 1973), where an immediate purpose was not evident.

Here, I examine the interactions of Great Blue Herons and various gulls, describe interaction types, determine interaction frequencies, and ascertain if all interactions are immediately purposeful.

Study area and methods.—All observations were at the 15.8 km² Yaquina Estuary (approximately 44°38′N, 124°03′W), on the midcoast of Oregon. From 1973 through 1981, I recorded over 1000 h of observations (including 745 60-min watches) of herons in intertidal areas as they foraged in the 3-h interval before and after low tide. Only interactions during 60-min watches were used to determine relative interaction frequencies, but notes from supplementary observations were used for other analyses. Sample sizes differ for various aspects of interactions because all characteristics of each interaction were not always recorded. All statistical tests are two-tailed.

Because of the frenzied activity generally accompanying interactions between herons and gulls, and because of the subtle plumage differences between Western Gulls (*L. occidentalis*), Glaucous-winged Gulls (*L. glaucescens*), Western × Glaucous-winged Gull hybrids (see Hoffman et al., Auk 95:441–458, 1978), Herring Gulls (*L. argentatus*), and Thayer's Gulls (*L. thayeri*), I was unable to distinguish among these species of gulls. My impression, however, was that 90% or more of these "large" gulls were Western Gulls or hybrids. Other

TABLE 1
TYPES OF INTERACTIONS OBSERVED DURING 60-MIN OBSERVATIONS

Gull taxon	Heron approaches gull				Gull approaches heron		
	N	% Cueing[a]	% Piracy attempt	% No food involved	N	% Piracy attempt	% No food involved
Large gull[b]	103	7	48	45	73	41	59
Ring-billed and California gulls	4	25	0	75	8	38	62
Mew Gull	5	20	20	60	2	100	0
Bonaparte's Gull	2	50	0	50	7	0	100
Total	114	9	45	46	90	39	61

[a] Cueing involves herons flying to a flock of feeding gulls; gulls did not cue to flocks of herons.
[b] Large gulls included mainly Western Gulls, Glaucous-winged Gulls, and Western × Glaucous-winged hybrids; some Thayer's Gulls and Herring Gulls may have also been included.

gulls that interacted with herons included Bonaparte's Gulls (*L. philadelphia*), Mew Gulls (*L. canus*), Ring-billed Gulls (*L. delawarensis*), and California Gulls (*L. californicus*).

Overt interactions included pursuit flights (i.e., one bird flying behind another flying bird), supplanting (i.e., an attacking bird flew, walked, waded, or ran towards a nonflying bird), "Swoop-and-soar" displays by gulls (see Tinbergen, The Animal in its World, Harvard Univ. Press, Cambridge, Massachusetts, 1972), or "Full forward" displays by herons (see Bayer, Colonial Waterbirds 7:45–54, 1984). If multiple attacks occurred within a min of each other, they were all classed as one interaction. An attack was considered to involve food piracy if one bird approached another bird that had food.

Frequency of interactions.—A total of 317 interactions between herons and gulls was recorded. The majority (86%) of interactions during 60-min watches involved large gulls (Table 1). The average frequency of interactions during 60-min watches of herons was 0.11/heron-h (SD = 0.41, N = 745 h), with territorial herons having an insignificantly higher frequency than nonterritorial herons. The infrequency of interactions was not due to a scarcity of either herons or gulls; both were present throughout the year, typically numbering over 100 individuals of each (unpubl. data). Most (54%) heron assaults involved gulls with food, while only 39% of gull attacks were on herons with food (Table 1).

Interactions involving food.—Gulls never joined heron feeding flocks. Herons rarely cued to (i.e., oriented to, approached, or joined) gull feeding flocks (Table 1); when they did, as many as 22 herons joined them. Most flocks of gulls were in water deeper than one m where herons could not feed.

Piracy attempts occurred when a heron or gull did not swallow food quickly (e.g., large prey with handling times > about 15 sec); then another bird had a chance to fly near the bird and attempt to steal its food. When a heron or gull with a large food item was approached, it often flew with the item held crosswise in its bill. Such birds seemed particularly susceptible to piracy because of their reduced maneuverability.

Piracy attempts by herons.—Although heron piracy attempts were usually infrequent (0.03/heron-h ± 0.13 [SD], N = 745 h), some territorial herons had rates as high as 4/h. Ninety-seven percent of 115 heron attacks were on large gulls; the remainder were on Mew Gulls and Ring-billed Gulls. Although 3–9 gulls were attacked in 29% of the attacks on large gulls, 54% of the attacks were on solitary gulls.

Only one heron at a time attempted to steal food from a large gull. In 84% of 81 attempts,

the gull flew away. A heron flight-pursued a large gull during a piracy attempt an average of 1.1 times (range = 1–3, N = 85). The average duration for each heron pursuit ranged from 3.0 to 80.0 sec with the mean duration for successful pursuits (19.4 sec ± 27.6, N = 6 attacks) not significantly different from unsuccessful ones (22.9 sec ± 20.5, N = 23) (t = 0.35, df = 27, $P > 0.10$).

Large gulls retained their food in 65% of 99 heron attacks, and herons ate stolen food after only 18% of these attempts. In 8% of these forays the food was lost to both the heron and the gull(s), and in 9% of the raids, herons obtained food but abandoned it. Territorial herons that attempted piracy twice or more per hour were successful in only 11% of 37 attempts, which was not significantly different from herons with lower attack frequencies ($\chi^2 = 3.02$, df = 1, $P > 0.10$). Herons assaulting solitary gulls were successful in 16% of 56 forays, which was not significantly different than for herons attacking groups of gulls (26% of 43 forays) ($\chi^2 = 2.02$, df = 1, $P > 0.10$).

Pirated food abandoned by herons included clams, large (i.e., >8 cm wide) starfish (*Pisaster* sp.), large pieces of carrion, and large crabs (*Cancer* sp.). These food items were probably too wide for a heron to swallow. Herons attacked gulls with such inappropriate prey in 29% of 72 attempts. In these instances, herons usually dropped the item and moved away, allowing the gull to reclaim the food; but two different territorial herons that had tried unsuccessfully to swallow robbed food defended it until encroaching gulls left, after which they moved away.

Piracy attempts by gulls.—Gull attempts at pirating herons were rare in Oregon (0.02/heron-h ± 0.11, N = 745 h) (this study), as well as in Nova Scotia (mean = 0.06/heron-h, N = 80 h) (Quinney et al. 1981). In Oregon, 85% of 34 piracy attempts were by large gulls, and the rest were by Mew, Ring-billed, or California gulls. Large gulls attempting to steal from a heron walked or flew toward the bird and tried to seize the item from the heron's bill. Usually, only one large gull attacked a heron, but as many as 4 gulls were sometimes involved. In 17% of 29 attempts by large gulls, the gulls were joined by a second heron that also attempted to steal the fish from the first heron.

Herons lost food during 13% of 30 gull piracy attempts; but because several gulls sometimes attacked a heron, the percentage of success per gull was only 8%. Only single large gulls were successful. The four successes included (1) an instance in which a gull waited until a heron abandoned a starry flounder (*Platichthys stellatus*) that was too large for the heron, (2) a gull eating young perch that were being born as a heron mandibulated a female live-bearing perch (family Embiotocidae), and (3) two instances of gulls quickly stealing fish that a heron had dropped on the mud to stab with its bill.

Attacks on gulls without food.— Seventy-three percent of 91 attacks by herons (all by solitary herons) were on large gulls, and the remainder were on Bonaparte's, Mew, Ring-billed, and California gulls. A solitary gull was assaulted in 63% of these attacks, but sometimes as many as 50 roosting gulls were involved.

Forty percent of the attacks occurred when a heron acquired a perching or foraging site. Herons were always successful in obtaining such sites from gulls. Although interspecific ardeid attacks in the tropics resulted in herons acquiring demonstrably better foraging sites (Caldwell 1980), Oregon herons did not catch significantly more prey in the 15-min period after an attack for a foraging site than they had before the attack (paired $t = 0.75$, N = 16, $P > 0.10$).

In 22% of these attacks, herons attacked gulls fighting among themselves. As fighting gulls vocalized similarly whether or not they had food, these attacks may have been mistaken piracy attempts.

Only 4% of these interactions could be classed as heron territorial defense. These were cases where a heron's pursuit ended when the gull passed the border of the heron's territory.

Such territorial defense was rare, as all gulls usually roamed over a heron's territory without assault, and some large gulls maintained feeding territories within that of a heron.

The purpose of the remaining 34% of heron assaults was not obvious, but seemed to be harrassment. These included three attacks by one heron on a pair of large gulls that were involved in courtship behavior (e.g., "Choking," and "Head-tossing," see Tinbergen 1972).

Attacks on herons without food.—Ninety-one percent of 47 gull attacks were by large gulls; the remainder were by Bonaparte's, Ring-billed, and California gulls. Gulls usually used the "Swoop-and-soar" display in attacking either flying or standing herons. Herons that were standing did not fly away but stayed and often directed "Full forward" displays at the attacking gull.

Gull attacks on herons were usually difficult to classify because no obvious purpose was apparent; however, in two interactions, herons that had initially disturbed gulls were outmaneuvered and subsequently pursued by a gull. In five gull attacks, a large gull could have been defending its nest against an approaching heron. Heron attacks on gull chicks were never observed, and gull chicks were not found as food given to heron young (unpubl. data). Herons have rarely been reported to prey on larid chicks (Chapman and Forbes, J. Field Ornithol. 55:251–252, 1984). The threat to gull chicks, however, may not have been as much predation as disturbance, which may cause chicks to wander from the nest, fall into the water, and drown (see Bayer, Murrelet 64:87–91, 1983).

The purpose of the remaining gull assaults seemed to be harrassment of flying herons. These included instances where large gulls, Ring-billed Gulls, and Bonaparte's Gulls forced a flying heron to change direction, to land in deep water (where the heron swam), or to find a nearby perch. Although gulls have been reported to prey on or kill other birds that they force into the water (Colston et al., Br. Birds 52:312–313, 1959; Boshoff, Cormorant 8:15–16, 1980), the attacked herons I watched seemed unharmed.

Conclusions.—Overt interactions were probably uncommon because they were not directly important for survival; only 48% of the interactions involved food (Table 1). Interactions did not result in greatly increased food availability, nor was either species a predator of the other. Gulls and herons did not forage similarly, so their interactions can not be ascribed to direct competition as have some interactions between other species (Roth, Wilson Bull. 90:450–451, 1978; Tye, Ibis 126:95–101, 1984).

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Circumstantial evidence of foraging interference between two species of dabbling ducks.—In a recent article on competition in bird communities, Maurer (Wilson Bull. 96:380–395, 1984) presents a verbal model that predicts the types of competition that can occur in different ecological settings. Maurer also calls attention to passive interference, a type of interspecific competition that may be important, but difficult to detect, in many bird communities. In this type of competition, direct aggression is rare, but interference occurs as resources are temporarily depressed by the activity of foraging individuals. In general, conclusive documentation of any competitive interaction in natural communities is difficult to achieve. Among the strongest evidence that empirical data can provide for competition

TABLE 1

SHIFTS IN FEEDING DEPTHS OF TWO SPECIES OF DABBLING DUCKS AND NUMBERS OF DUCKS DURING FOUR OBSERVATION PERIODS

Date of observation periods	Order of recording events	Average feeding depth (cm)		Individual number		
		Teal	Shoveler	Teal	Shoveler	Total[a]
27 July	1.	4.9 (65)[b]	13.5 (120)	3	10	19
	2. (60)[c]	4.7 (150)	16.0 (20)	15	2	28
	3. (85)	7.1 (45)	20.5 (12)	15	4	32
	4. (125)	17.0 (252)	20.2 (80)	15	1	24
28 July	1.	4.7 (60)		3	0	3
	2. (40)	10.9 (326)	19.9 (189)	35	6	45
	3. (120)	11.9 (157)	19.1 (139)	23	5	40
29 July	1.	8.3 (30)		3	0	3
	2. (25)	10.8 (479)	17.2 (217)	44	9	72
30 July	1.	8.2 (121)	16.5 (35)	24	7	32
	2. (120)	19.0 (609)	24.2 (206)	65	15	82

[a] Individuals of dabbling duck species other than teal and shoveler are also included if present.
[b] Number of feeding method observations; see Study area and methods for calculation of feeding depths.
[c] Minutes since beginning of the first recording event; when calculating correlations a value of 0 was given to the first event.

is niche shifting, where the presence of a putative competitor gives rise to a shift in the resource use of the target species (cf. Werner and Hall, Science 191:404–406, 1976; Diamond, Am. Sci. 66:322–331, 1978; Thomson, Am. Nat. 116:719–726, 1980; Alatalo, Oikos 37: 335–344, 1981). The purpose of this note is to provide an example of possible passive interference competition between two species of dabbling ducks, the Green-winged Teal (*Anas crecca*) and the Northern Shoveler (*A. clypeata*). I used shifts in depths at which the species fed as indicators of interaction.

Study area and methods.—The study was conducted at a shallow (0.5 to 0.7 m), eutrophic bay of Lake Simpele in SE Finland (61°33′N, 29°33′E). More detailed information on the study area can be found in Pöysä (Oikos 40:295–307, 1983a). All the data are from a small (ca. 0.67 ha) and closed bay of open water, where the submerged vegetation is rich from the bottom to the surface (feeding habitat type A in Pöysä 1983a). The data for this note were gathered between 27 and 30 July 1980. The use of such a short time period minimized possible intrinsic changes in food resource conditions, making the interpretation of changes in the foraging behavior of the ducks more accurate. Each day, during an observation period of from 25 to 125 min, I recorded at an average of 56 ± 13-min intervals, the numbers of foraging individuals present for each species and their feeding methods.

Dabbling ducks in the study area comprised 6 species, the other 4 being Eurasian Wigeon (*A. penelope*), Mallard (*A. platyrhynchos*), Northern Pintail (*A. acuta*), and Garganey (*A. querquedula*) (Pöysä 1983a; Ornis Scand. 14:317–326, 1983b); however, as the number of observations was too low for these 4 species, they were not included here. Feeding methods included up-ending, neck submerged, head submerged, bill submerged, picking from surface, and straining from surface. The average number of feeding method observations per individual at a given recording event was 11.2 ± 1.8 in the Green-winged Teal and 23.0 ± 7.9

in the Northern Shoveler. Average feeding depths of the species at a given recording event were calculated on the basis of feeding method and morphological (body length, neck length, skull length, bill length) data, following the procedure described in Pöysä (1983b). For the birds picking and straining from surface, I assumed a feeding depth of 1.0 cm.

Results.—During each observation period the average feeding depth of the species increased from the first recording event onward (Table 1). Both in teal and shovelers, a significant positive correlation existed between the average feeding depth and the time since the start of the observation period ($r = 0.72$, N = 11, $P < 0.05$ for teal; $r = 0.76$, N = 9, $P < 0.05$ for shovelers) (Table 1). The average feeding depth of teal also correlated significantly with the number of teal present ($r = 0.70$, N = 11, $P < 0.05$) as well as with the total individual number of dabbling ducks present ($r = 0.63$, N = 11, $P < 0.05$), but not with the number of shovelers present ($r = 0.41$, N = 11, $P > 0.05$). By contrast, the average feeding depth of the shoveler correlated significantly with the number of teal ($r = 0.76$, N = 9, $P < 0.05$), but not with the number of shovelers ($r = 0.20$, N = 9, $P > 0.05$) or all dabbling ducks ($r = 0.57$, N = 9, $P > 0.05$).

Discussion.—The results demonstrate an increase in the feeding depth of shovelers with the presence and increasing numbers of teal. In teal, however, the negative effect of shovelers was minimal, possibly due to the low number of shovelers present; and significant interference was observed only intraspecifically. Moreover, the longer individuals of both of these species spent foraging in the patch, the greater was the shift toward greater feeding depths. These findings support the presence of an interactive shift in feeding depth, as during observation periods as short as those used here, intrinsic (i.e., not caused by the foraging ducks) changes in resource conditions should be minimal. Both passive interference and exploitation (cf. Schoener, Am. Nat. 122:240–285, 1983; Maurer 1984) might have been involved as mechanisms of interaction. When the average feeding depths of teal are compared between the first recording event of a particular observation period and the last recording event of the previous observation period, we see that the profitability of the surface layer has returned. Even though direct measurements of food availability and replenishment were not made, I tentatively suggest that the food resource was not replenished, but that availability of the prey was at least in part temporarily depressed as a result of disturbance of actively moving, foraging dabbling ducks. As the number of foraging ducks at most recording events was large (see Table 1), direct removal and consumption of prey by ducks also was probably important. Further examples of passive interference in other groups have been reported by Goss-Custard (Ardea, 68:31–52, 1980) for wading birds, and by Waite (Behav. Ecol. Sociobiol. 15:55–59, 1984) for corvids.

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Band-rumped Storm-Petrel occurrences in relation to upwelling off the coast of the southeastern United States.—In spite of several storm-related and stranding records of Band-rumped Storm-Petrels (*Oceanodroma castro*) in eastern North America since 1900 (reviewed by Clapp et al., Marine Birds of the Southeastern United States and Gulf of Mexico, Pt. 1, Gaviiformes through Pelecaniformes, U.S. Fish and Wildl. Serv., Washington, D.C., 1982), over 90% of the marine occurrences of the species have been recorded since 1980 (Haney, Oriole 48:21–32, 1983; Lee, Am. Birds 38:151–163, 1984; Sykes et al., Fla. Field Nat. 12:

17–18, 1984). During 1983 and 1984, seabird surveys in the South Atlantic Bight (Cape Hatteras, North Carolina, to Cape Canaveral, Florida) were made during investigations of boundary current upwelling on the outer continental shelf and slope. These studies, which incorporated synoptic coverage of water masses with satellite imagery, indicated that Band-rumped Storm-Petrels exhibit a marked affinity for centers of localized upwelling where food is plentiful. The association of Band-rumped Storm-Petrels with upwelling centers is discussed here in context of suggestions that the species occupies an ecological niche in water masses of low biological productivity in the Atlantic Ocean (Cramp and Simmons, The Birds of the Western Palearctic, Vol. 1, Oxford Univ. Press, Oxford, England, 1977), and is restricted to warm, pelagic marine habitats (Lee 1984).

Methods.—Seabird surveys were conducted using 15-min count periods and a 300-m band transect (Tasker et al., Auk 101:567–577, 1984). Between April 1983 and October 1984, 1217 counts were made on the outer shelf (40–200 m depth, N =667) and upper slope (200–1000 m, N = 550) of the study area (29° to 33°N latitude). Identifications of Band-rumped Storm-Petrels were based largely on behavioral field marks (Brown, Br. Birds 73:263–264, 1980; Naveen, Birding 14:10–14, 1982; Harrison, Br. Birds 76:161–174, 1983). Observations of one or more individuals (numbers listed chronologically by calendar date) were made on 29 April (1), 30 April (3), 1 May (5), 2 May (3), 7 June (2), 13 June (1), 11 July (1), 12 July (1), 1 August (18), and 2 August (1) 1984; and on 30 August (1) and 4 September (1) 1983. Sea surface temperature (SST) and depths were measured with a continuously recording thermosalinograph and white-line fathometer, respectively, at each sighting.

Upwelling was identified by satellite-derived data in conjunction with shipboard measurements. Surface-manifested upwelling on the outer shelf and upper slope in the South Atlantic Bight may stem from two fundamental sources: Gulf Stream filament eddies (Atkinson, Geophys. Res. Lett. 4:583–586, 1977) and where topographic features of the western Blake Plateau (upper slope) deflect or alter the Gulf Stream flow (Legeckis, J. Geophys. Res. 9:483–497, 1979). Gulf Stream filament eddies were identified with 1983–1984 Gulf Stream System Flow Charts (N = 215; NOAA, Miami, Florida) based on very high resolution infrared satellite imagery. Between 31 July and 2 August 1984, SST isotherms were mapped and seabird counts conducted at an eddy off the Georgia coast. Topographic upwelling was centered mainly at the Stetson Mesa (30°30′N, 79°30′W) and Hoyt Hills (32°00′N, 78°30′W). Upwelling at these sites was detected with vertical temperature profiles derived from deep-water, expendable bathythermograph (XBT) grids.

Results.—Band-rumped Storm-Petrels were observed on only three of nine cruises during 1983 when surveys were confined to the continental shelf, but were seen on each of five cruises to the upper slope in 1984. The storm-petrel was observed mainly off Florida and Georgia where survey effort was most intensive (Fig. 1). Environmental measurements confirmed the species' affinity for warm, pelagic water masses (Lee 1984). Band-rumped Storm-Petrels were not observed in deep water east of the Gulf Stream on the middle Blake Plateau (Fig. 1).

Lee (1984) reported Band-rumped Storm-Petrels at sea surface temperatures (SST) of 26.8° to 28.4°C off North Carolina; 95% of individuals (N = 75) were in waters > 900 m. In contrast, 90% of individuals (N = 38) I observed occurred over shallower waters, <900 m ($\bar{x}$ = 515 ± 209 [SD]), where SSTs ranged from 25.5° to 29.0°C ($\bar{x}$ = 27.4 ± 1.3). As the sightings I made came from a more extended period (29 April to 4 September vs 30 May to 20 August), part of the greater SST range may be attributed to seasonal warming of water masses (Atkinson et al., J. Geophys. Res. 88:4705–4718, 1983). Lee (1984) suggested that depth was a key factor in the distribution of this species. My data indicate that its meso-scale (10–100 km) distribution may not be correlated with depth or SST per se, but rather to dynamic upwelling processes, which in turn affect local productivity and food availability.

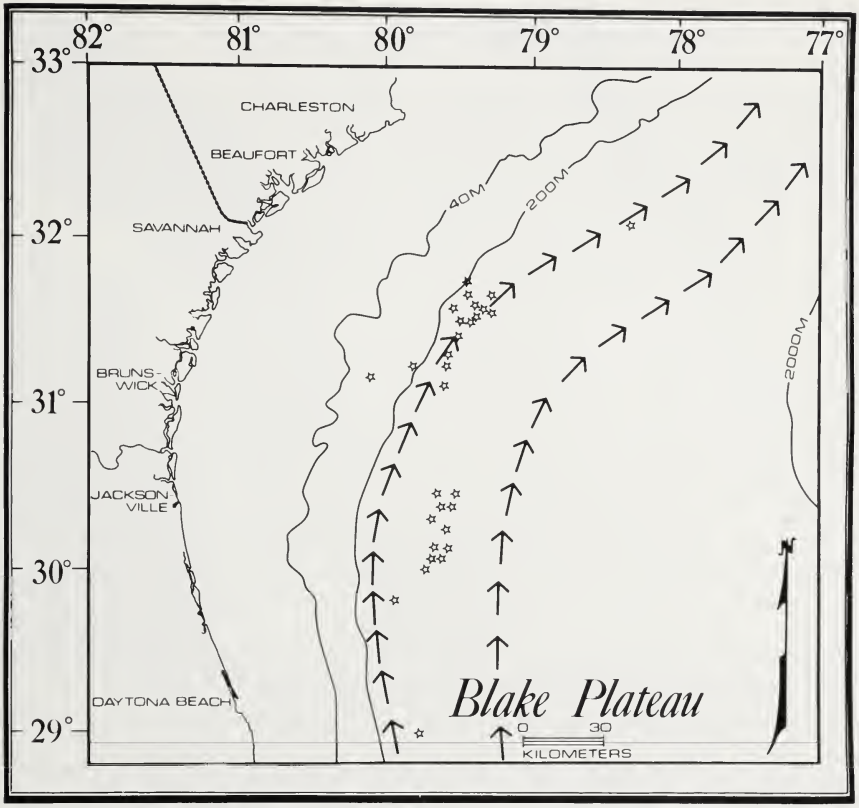

FIG. 1. Locations of Band-rumped Storm-Petrel observations in the South Atlantic Bight, 1983–84. Annual mean positions of the western and eastern Gulf Stream current boundaries are shown by arrows.

Upwelling occurs, however, at different cross-shelf/slope locations in pelagic waters off the southeastern United States as a result of interregional differences in bathymetry, and in the position of the western Gulf Stream front.

Nearly 90% of individuals and 75% of occurrences were associated with locations of upwelling. Sixty-one percent of individuals and 42% of occurrences (N = 12) were at Gulf Stream eddies. Twenty-nine percent of individuals and 33% of occurrences were at topographic upwelling sites. During a cruise across the Georgia continental shelf and slope, 31 July to 2 August 1984, I observed Band-rumped Storm-Petrels exclusively in the cold core of a Gulf Stream filament eddy (Fig. 2). Upwelling in eddy cores results in 10–100 fold increases in primary production compared to adjacent Gulf Stream and resident shelf waters (Yoder et al., Limnol. Oceanogr. 26:1103–1110, 1981). The resident high phytoplankton biomass provides forage for zooplankton and nekton, including small myctophid fish, squid, amphipods, and euphausiids (P. McGillivary, pers. comm.). These items may on occasion comprise the diet of Band-rumped Storm-Petrels (cf. Harris, Proc. Calif. Acad. Sci. 37:95–

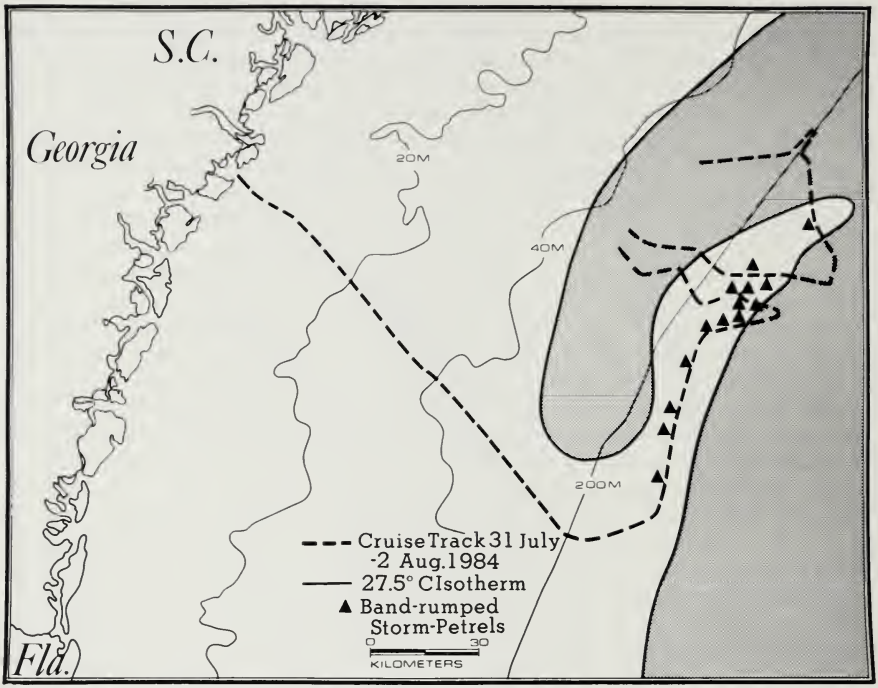

FIG. 2. Band-rumped Storm-Petrel distribution in relation to a Gulf Stream filament eddy. Shaded region is surface Gulf Stream water (>27.5°C) and unshaded region is either shelf or colder, upwelled subsurface Gulf Stream water (<27.5°C). Upwelling occurs in the eddy cold core, between the filament of warm water and the main body of the Gulf Stream. The 27.5°C isotherm defines a region of maximum, horizontal SST gradient between the water masses.

166; Lee 1984). Seabird densities in the cold core are 10–20× higher than in adjacent waters (Haney, unpubl. data), further attesting to the significance of eddy-associated upwelling for marine organisms.

The biological conditions stemming from upwelling are not available continually for foraging storm-petrels in the South Atlantic Bight. Gulf Stream eddies, for example, are small features (20–50 km wide, 70–120 km long) that form and degrade in 2 to 14 days, and move northward with the Gulf Stream at 35 to 40 km/day (Lee and Brooks, Geophys. Res. Lett. 6:321–324; Blanton et al. 1981; Lee et al. 1981). These upwelling events are nonseasonal, and at any given time eddies (and upwelling) may be present along the outer shelf and upper slope between North Carolina and Florida.

Discussion.—Storm-petrels show widespread affinities for regions of upwelling (Gould, Ph.D. diss., Univ. Arizona, Tucson, Arizona, 1971), including upwelling at small-scale features (e.g., submarine canyons in the Pacific; Stallcup, West. Birds 7:113–136, 1976). Patchy, localized upwelling could account for the occurrence of Band-rumped Storm-Petrels elsewhere in western North Atlantic waters off the southeastern United States. Blanton et al. (Deep-Sea Res. 28:393–405, 1981) describe upwelling induced by a combination of Gulf

Stream flow and the diverging isobaths "downstream" (north) of Cape Canaveral, Florida. Virtually all North Carolina sightings of Band-rumped Storm-Petrels occurred downstream of the diverging isobaths north of Cape Hatteras (Lee 1984) (Fig. 1). Both regions contain similar bathymetry and both are strongly influenced by eastward Gulf Stream meanders that cause upwelling (Atkinson 1977; Lee et al., Deep-Sea Res. 28:347–378, 1981). Prior to 1984, more records of Band-rumped Storm-Petrels existed for the Gulf than the Atlantic coast of Florida (Sykes et al. 1984). Eddies of the Loop Current in the northeast Gulf of Mexico cause upwelling off western Florida, providing similar physical and biological conditions to those in the South Atlantic Bight (Paluszkiewicz et al., J. Geophys. Res. 88:9639–9651, 1983). The occurrence of Band-rumped Storm-Petrels in this region has been considered underestimated due to lack of observation and misidentification (Clapp et al. 1982).

Band-rumped Storm-Petrels are more solitary than the other Atlantic storm-petrel species (Cramp and Simmons 1977), and may more frequently exploit the localized and transitory patches of productivity found in tropical and subtropical water masses off the southeastern United States. Although I also observed Leach's (*O. leucorhoa*) and Wilson's storm-petrels (*Oceanites oceanicus*) at upwelling sites, their abundance relative to *Oceanodroma castro* was low compared to the abundances of these storm-petrels elsewhere in the Atlantic. For instance, at the eddy studied 31 July to 1 August 1984 (Fig. 2), 38% of 45 storm-petrels were *castro,* compared to 58% *oceanicus* and 4% *leucorhoa.* Leach's and Wilson's storm-petrels were common in the study area only during spring migration (May–June). The occurrence of Band-rumped Storm-Petrels in these generally oligotrophic water masses may lend support to previous speculations regarding the species as a low-density occupant of the Atlantic Ocean where other storm-petrels are scarce (Cramp and Simmons 1977, Naveen 1982).

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Nest, seasonal movements, and breeding of Buffy Hummingbirds in xeric habitats of northeastern Venezuela.—The Buffy Hummingbird (*Leucippus fallax*) is restricted to the ". . .arid Caribbean littoral of Colombia in eastern Santa Marta and the Guajira Peninsula eastward along the Venezuelan coast to Sucre. . ." and some islands off northeastern Venezuela (Meyer de Schauensee, The Species of Birds of South America and their Distribution, Livingston, Narberth, Pennsylvania, 1966). The species also occurs farther inland (e.g., in the State of Lara; Phelps and Phelps, Bol. Soc. Venez. Cienc. Nat. 90:1–337, 1958). It

inhabits xerophytic areas and thorn scrub from sea level to 550 m and mangroves (Meyer de Schauensee and Phelps, A Guide to the Birds of Venezuela, Princeton Univ. Press, Princeton, New Jersey, 1978). The disjunct distribution of the three recognized subspecies (Phelps and Phelps 1958) largely corresponds to the discontinuous distribution of open xerophytic areas with bare soil, thorn scrub, and thorn forests (Anonymous, Atlas Forestal de Venezuela, Ministerio de Agricultura y Cria, Caracas, 1961; Sarmiento, J. Ecology 60: 367–410, 1972).

Although the Buffy Hummingbird is one of the commonest hummingbirds of the coastal xerophytic habitats of northern South America, little has been published about its biology apart from the observations by Robinson (Robinson and Richmond, Proc. U.S. Natl. Mus. 18:649–685, 1895) on its habitat, food, song, and nest on Margarita Island. Virtually nothing is known of the biology of any *Leucippus* other than that they inhabit scrub habitats (J. V. Remsen, pers. comm.). *L. baeri* and *L. taczanowskii* inhabit arid scrub in western Peru (Schulenberg and Parker, Condor 83:209–216, 1981), and *L. chlorocercus* apparently is restricted to early successional scrub along rivers in western Amazonia (Remsen and Parker, Biotropica 15:223–232, 1983).

From May 1965 through June 1967, we gathered data on the biology of *L. fallax richmondi,* the form that breeds in northeastern Venezuela and on Margarita Island (Phelps and Phelps 1958).

Breeding habitat.—In northeastern Venezuela, the Buffy Hummingbird breeds in cactus or thorn scrub as defined by Sarmiento (pp. 65–99 *in* Evolution of Arid Vegetation in Tropical America, D. W. Goodall, ed., Univ. Texas Press, Austin, Texas, 1976), dominated by various genera of Cactaceae (*Lemairocereus, Pereskia, Cephalocereus, Acanthocereus, Opuntia, Melocactus,* etc.) along with *Acacia* and *Prosopis* (Mimosaceae), *Parkinsonia* and *Cercidium* (Caesalpiniaceae), *Croton* (Euphorbiaceae), and *Capparis* (Capparaceae) (McNeil, unpubl.).

Nest.—Two nests were found on 25 May 1967 in Cumaná (State of Sucre). The first, containing two nestlings, was found 2 m above the ground saddled upon a branch of *Platymiscium diaphanum* (Fabaceae) near a house. The incubating bird was so fearless (see also Robinson and Richmond 1895) that it allowed itself to be photographed at a distance of 30 cm (Fig. 1A). It sat with its tail high in the air and its wings beneath the tail. When revisited 2 weeks later, the nest was empty. The second nest, which was found empty about 50 m from the first one, was in the fork of a branch 1.5 m high in a *Capparis pachaca.* Both nests were collected by the first author and were deposited in the ornithological collection of the Université de Montréal (Catalogue Nos. 01129 and 01130). At the end of November 1982, the second author found a third nest containing two nestlings. It rested on a branch of *Pithecellobium pubescens* (Mimosaceae), 2 m above the ground, in a desert close to Chacopata Lagoon, on the north side of the Araya Peninsula (State of Sucre).

The nests are hollow basket structures, i.e., typical hummingbird nests (Fig. 1A, B). The dimensions for Nos. 01129 and 01130 (Cumaná) and the Chacopata nest are, respectively: outside diameter, 3.2, 2.7 and 3.0 cm; height, 4.2, 4.0, and 4.0 cm; inside depth, 2.1, 2.0, and 2.0 cm. All three were constructed and attached to the branch with a fine, white, soft material (Fig. 1B). These fibers came from the fruit (Fig. 1C) of *Gossypium arboreum* (Malvaceae), a scrub in the bird's breeding habitat. The nest from Chacopata was covered

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FIG. 1. Nest of Buffy Hummingbird in Cumaná, Sucre, Venezuela, 25 May 1967: (A) a side view showing an incubating bird, (B) interior view showing the material with which the nest is made and the nestlings, and (C) cotton-wool of *Gossypium arboreum.*

A
B
C

outside entirely with pieces of bark and bark lichens, apparently taken from the nest tree; the other two were covered on the outside with leaf debris and other small plant fibers and fragments, including small pieces of bark and bark lichens. The nest found by Robinson (Robinson and Richmond 1895) was ". . . saddled upon the branch of a small nettle bush only 2 feet from the ground . . ." and was also covered with lichens, although Yepez (Mem. Soc. Cienc. Nat. LaSalle 67:5–39, 1964) seems to question this.

Timing of breeding.—According to Robinson and Richmond (1895), *L. fallax* is not found where cacti do not occur in abundance, and is therefore strictly limited to the coast region. In Cumaná, Buffy Hummingbirds are present all year long in cactus or thorn scrub, but they are more abundant (No. of birds/net/day during 2-day netting periods every 2 or 3 weeks) from August to October (McNeil, unpubl.). Most individuals (38 of 46 captured birds) were in heavy molt (tail, body, and wings) from the end of July to mid-October. Brood patches were found on 6 heavily molting birds in the first half of September. These data, along with those from the 2 above-mentioned occupied nests (25 May and end of November) and that found in a similar habitat on 20 July by Robinson (Robinson and Richmond 1895), suggest that reproduction in this species is at its peak from May to the end of July and declines thereafter, but may occur on rare occasions into late November.

Seasonal movements.—In the area west of Cumaná, the cactus or thorn scrub plant formation constitutes only a narrow fringe between the sea and the thorn forest formation beginning on the lower slopes of the contiguous coastal mountains. The thorn forest is dominated by species of *Belencita* and *Morisonia* (Capparaceae), *Beureria* (Ehretiaceae), *Acacia, Capparis, Croton,* and *Pereskia* along with scattered individuals of the above-mentioned genera of Cactaceae. Floristically, the thorn scrub seems to be an impoverished thorn forest; Cactaceae, Capparaceae, Euphorbiaceae, and Momosaceae continue to be the best-represented taxa, but succulent species, particularly cacti, appear here at their optimum (Sarmiento 1976).

Buffy Hummingbirds seem to occur in coastal thorn forests mainly during the nonreproductive season. In fact, other mist-netting data obtained from May 1965 through June 1967 near Cumaná show that in that habitat *L. fallax* is absent or almost absent from May through October but is abundant from mid-October to the end of January, and then decreases thereafter until May. The Buffy Hummingbird appears to be the only trochilid species present in this habitat from the beginning of January to mid-April. Only one of 37 birds mist netted in October was molting, but 13 of 39 taken from 7 November to mid-December showed heavy molt.

These data suggest that by the end of the rainy season, which extends from mid-April to the end of November, many Buffy Hummingbirds leave the more arid xerophytic areas (thorn scrub) and move to thorn forest where they are not known to breed regularly. Several hummingbird species are known to show seasonal movements in the Neotropics (Colwell, Am. Nat. 107:737–760, 1973; Feinsinger, Ecol. Monogr. 46:257–291, 1976). The almost total absence of Buffy Hummingbirds from thorn forest between May and October coincides with the invasion of the habitat by other trochilid species (e.g., Ruby-topaz Hummingbird *Chrysolampis mosquitus,* Copper-rumped Hummingbird *Amazilia tobaci,* Blue-tailed Emerald *Chlorostilbon mellisugus,* and Rufous-breasted Hermit *Glaucis hirsuta*) which inhabit these areas during the rainy season (McNeil, unpubl.).

That pattern in *L. fallax* may also result from seasonal variations in the sources of food (see Colwell 1973). Robinson and Richmond (1895) found that Buffy Hummingbirds eat not only juice but also the flesh of the fruits of *Lemairocereus,* as well as the nectar of the waxlike, coral-red flowers of melon cactus (*Melocactus*), and the flowers of tuna (*Opuntia*) and cardones (*Lemairocereus*). Stomach-content analysis shows that from mid-October to the end of January, when cacti fruits are not available, *L. fallax* feeds on insects (B. Poulin

and G. LeFebvre, pers. comm.), which are presumably more abundant in thorn forest than in thorn scrub during the dry season.

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Brood-rearing and postbreeding habitat use by Virginia Rails and Soras.—Virginia Rails (*Rallus limicola*) and Soras (*Porzana carolina*) are abundant summer residents in upper midwestern marshes. Relatively little is known of their ecology because of their secretive nature and the dense vegetation that they inhabit. Recent research has focused on their breeding habitat (Weller and Sparcher, Iowa Agric. and Home Econ. Exp. Stn. Spec. Rep. 43, 1965; Andrews, M.S. thesis, The Ohio State Univ., Columbus, Ohio, 1973; Baird, M.S. thesis, Fort Hays State College, Fort Hays, Kansas, 1974; Tacha, M.S. thesis, Fort Hays State College, Fort Hays, Kansas, 1975; Griese et al., Wilson Bull. 92:96–102, 1980; Johnson, M.S. thesis, Iowa State Univ., Ames, Iowa, 1984), but their brood-rearing and postbreeding habitat use and movements are virtually unknown. In 1982, a biotelemetry study was conducted to identify these features of their ecology.

Study area and methods.—The study was conducted on Dewey's Pasture and Spring Run Game Management Areas in northwestern Iowa. Dewey's Pasture is a 136-ha wetland complex in Clay and Palo Alto counties (Weller, Proc. Iowa Acad. Sci. 86:81–88, 1979), including 45 ha of seasonal and semipermanent marshes. Dewey's Pasture wetlands are dominated by emergent stands of cattail (*Typha glauca*), sedges (*Carex* spp.), bulrushes (*Scirpus acutus, S. fluviatilis*), and bur reed (*Sparaganium eurycarpum*). Spring Run in Dickinson County covers roughly 200 ha. Krapu et al. (Iowa State J. Res. 44:437–452, 1970) describe the upland vegetation. Marshes are dominated by cattail, sedges, bur reed, and willows (*Salix* spp.), and are flooded seasonally or semipermanently.

Incubating and brood-rearing Virginia Rails and Soras were located by walking through marshes near known rail territories (Johnson, 1984) and listening for the adult alarm calls (Kauffmann, Wilson Bull. 95:42–59, 1983). A trap consisting of a catch box (Baird, 1974) placed at the apex of a "V" formed by two leads of poultry netting was constructed near the calling adult. Rails were driven into the trap by dragging a rope weighted with rock-filled cans and jugs through the emergent vegetation toward the trap.

Captured rails were banded with U.S. Fish and Wildlife Service bands and sexed using characteristics described by Horak (M.S. thesis, Iowa State Univ., Ames, Iowa, 1964). Captured rails were equipped with AVM single-stage transmitters powered by a single Hg575 or Hg41 battery. The transmitting antenna consisted of a 15-cm stainless-steel guitar string. The entire package, encapsulated in Hysol epoxy, weighed 3.6–4.0 g. Estimated package life based on battery size and current drain of individual transmitters was 67–90 days.

The transmitter was held in place by clipping the feathers of the mantle and gluing the package to the skin with commercial eyelash cement. The package was also attached by a harness of braided nylon cord, which was tied around the birds.

Rails with transmitters were relocated at 2-day intervals with an AVM LA-12 receiver and a hand-held Yagi antenna. Locations were plotted on cover maps prepared from aerial photos of the study areas. On 1 August 1982, the Spring Run area was searched from the air.

Results.—From 25 May to 6 July 1982, 10 birds of each species (5 males and 5 females) were equipped with transmitters. Transmitters weighed from 3.9 to 4.4% of rail body weights. The mean duration of contact with birds with transmitters was 27 days ± 16 [SD]. Contact was lost because of transmitter failure (preceded by an irregular pulse or continuous signal) or the emigration of birds from the study area.

Two brood-rearing female Soras dispersed within 4 days of capture, evidently in response to investigator disturbance. Each was relocated away from the nest vicinity once before contact was lost permanently. A female Virginia Rail died when her transmitter antenna became tangled in vegetation.

Both Virginia Rails and Soras raise their broods to independence as a family group on the breeding territory. Estimates of the home range size were obtained by plotting the outermost locations for both species. The size of this brood-rearing home range is similar to estimates of the size of the breeding territory (Glahn. Wilson Bull. 86:206–214, 1974). Virginia Rails and Soras occupy small brood-rearing home ranges of similar size (0.18 ha ± 0.02 [SE] and 0.19 ha ± 0.02, respectively). Home ranges were similar for both sexes. The home ranges of male and female Virginia Rails covered 0.16 ha ± 0.03, and 0.22 ha ± 0.07, respectively. Sora males and females maintained home ranges of 0.17 ha ± 0.03, and 0.22 ha ± 0.01, respectively.

Both members of three Virginia Rail pairs and one Sora pair were captured and equipped with transmitters. Home ranges of paired males and females typically overlapped extensively. The only exception was one pair of Virginia Rails whose combined home range followed the contours of a band of emergent vegetation bounded by upland and open water. The two home ranges formed two equally long arms of a "V." Each sex occupied one arm, and the home ranges overlapped only at the apex. Locations for both members of the pair were uniformly distributed throughout their home ranges, and no preponderance of locations occurred at the apex. Earlier, this pair occupied a large breeding territory, which may have allowed a greater degree of pair member segregation.

Home ranges during brood-rearing typically were bounded by open water and upland. As with breeding rails, no significant preference was exhibited for any species of emergent vegetation on the home range (Johnson, 1984; Johnson, Ecology 61:65–71, 1980). Cover was used as available. The size of home ranges during brood-rearing was not correlated with cover type diversity for either species ($P > 0.10$) (Snedecor and Cochran, Statistical Methods, Iowa State Univ. Press, Ames, Iowa, 1967). Territories and home ranges were seldom located over water shallow enough for rails to wade; rather, rails moved about on floating vegetation.

The movements of postbreeding Virginia Rails and Soras preceding migration have been poorly documented. Hon et al. (Proc. Ann. Conf. S.E. Assoc. Fish and Wildl. Agric. 31:72–76, 1977) found that the average dispersal distance of 6 coastal Clapper Rails (*Rallus longirostris*) banded in Georgia in March through August, and shot away from the banding site, was 51 km. It is not clear how the movements of postbreeding birds of that presumably nonmigratory population compare with those of migratory Virginia Rail and Sora populations in Iowa.

We maintained contact with 16 birds with transmitters (8 Virginia Rails and 8 Soras)

until late July 1982 when they emigrated. During that time, a female Virginia Rail, already discussed, died after leaving her mate and dispersing from the vicinity of the nest, and a transmitter on a female Sora failed.

At both sites, birds with transmitters left the home ranges they used during the breeding season. Between 19 July and 1 August 1982, 7 Virginia Rails (5 males, 2 females) and 7 Soras (5 males, 2 females) dispersed from their home ranges.

The first dispersal-like movements were recorded on 12 July, when 2 unrelated Virginia Rails (1 male, 1 female) left the nest vicinity. The male was found moving along a sparsely vegetated road ditch 150 m N of previous locations. On 14 July, he was located 100 m E of the nest vicinity, across a gravel road that had previously been a boundary of his home range. He remained there until contact was lost on 19 July. On 12 July a female Virginia Rail moved her brood over 3 days to a small temporary wetland 400 m from her former home range. Another male Virginia Rail was relocated repeatedly as he moved through study area wetlands. Contact was initially lost on 19 July and was reestablished on 20 July on a semipermanent wetland 600 m N of his home range during brood-rearing. On 26 July, he was relocated 550 m SW of that location. Within 2 days, he had moved 175 m NNW. On 1 August 1982, he was located 2.3 km N of the 28 July location (2.6 km N of his home range during brood-rearing).

On 1 August a total of 522 km^2 surrounding the Spring Run area, including concentrations of nearby wetlands, was searched from the air. A Sora male, originally lost on 19 July, was relocated 4.8 km ESE of the study area in a soybean (*Glycine max*) field, approximately 300 m from a large seasonal wetland. A subsequent ground search for this bird indicated that he was moving. No other rails whose transmitters' signals were lost in late July were relocated in this search.

Adults remained on the brood-rearing home range until Virginia Rail young were 15–42 days old ($\bar{x}$ = 25, N = 7) and Sora chicks were 16–32 days old ($\bar{x}$ = 23, N = 5). Most adults emigrated from their home range when their broods were 15–21 days old. The movement of the young at the time of adult emigration is unknown. A fledgling Sora male, the only young-of-the-year with a transmitter, was captured on a Sora breeding territory on 6 July, and remained there until 23 July.

The movements of single pairs of Virginia Rails and Soras suggest that the pairbond breaks down before extensive dispersal occurs. A female Virginia Rail left her mate on 12 July and moved her 17-day-old brood to a weedy cornfield (*Zea maize*) 200 m SW of the former home range. She and her brood remained in the cornfield until 14 July, they then moved 250 m SSW to a temporary wetland where she remained on the upland-wetland interface for 4 days until she died on 18 July. Her mate remained on the family's home range until 26 July. This Sora pair raised their brood to 17–20 days (21 July), at which time the male moved across a gravel road, previously a boundary of the home range, to a 3-ha semipermanent wetland and established a home range 150 m from the female. He remained there until 5 August when contact was lost. His mate remained on the initial home range until 26 July, when she emigrated.

Discussion.—Monitoring the movements of Virginia Rails and Soras indicates that both species raise their broods on a highly localized home range, which was previously the breeding territory. Kauffmann (Ph.D. thesis, Univ. Minnesota, Minneapolis, Minnesota, 1971) noted that 3 family groups of Virginia Rails remained on their breeding territories up to 20 days after hatching, and abandoned the sites only when the marsh was nearly dry. He also noted that chicks older than one week spread out in the home range, stay within its boundaries, and are near an adult only for brooding or feeding. He noted that chicks are fed until they are 2–3 weeks old. Begging by older chicks frequently resulted in attacks by the male. Pospichal and Marshall (Flicker 26:2–32, 1954) observed 1- to 2-week-old Virginia Rail

chicks with adults, but older chicks were not seen with adults. They also noted that at 25 days Sora chicks had almost full juvenal plumage and were independent.

Irish (Jack-Pine Warbler 52:115–124, 1974) interpreted Virginia Rail and Sora responses to tape-recorded calls in July and August as defense of a postbreeding territory, though little evidence is presented to support this hypothesis. By contrast, we observed that chasing and posturing in response to taped calls, the primary means of territory defense (Kauffmann 1983), were rare within several weeks after territory establishment. The frequency of responses to taped calls declined as hatching approached (Johnson 1984). The observations made by Irish (1974) may correspond to the second peak in calling activity observed by Pospichal and Marshall (1954), Glahn (Wilson Bull. 86:206–214, 1974), and Kauffmann (1971). No clearly defined second peak was observed in this study.

Adult Virginia Rails and Soras made a previously unreported dispersal from the vicinity of the home range used for brood-rearing. We believe the stimulus for this emigration is the maturation and increasing independence of the brood. The adult male may stimulate the breakdown of the family group with increasing aggressiveness toward the chicks and his mate. Kauffmann (1971), noting that juvenile and adult rails were always observed alone during late summer, suggested that this solitary behavior was due to increasing aggressive behavior of the chicks. We were unable to determine which sex emigrated from the home range first.

When emigration or dispersal does occur, it appears to involve a fairly long-distance movement between wetlands. Pospichal and Marshall (1954) noted that, in late summer, rails left wetlands for short periods to feed on uplands. Upland areas, including row crops, may serve as initial dispersal habitat. A female Virginia Rail and her brood used a weedy cornfield for 2 days before returning to wetland habitat. A Sora, located after dispersal near an isolated seasonal wetland 5 km from his home range, must have made extensive use of row crops in the 12 days after dispersal and, indeed, was relocated in a soybean field.

The significance of this dispersal is unclear. It may simply act to segregate family members because of increasing aggressiveness, it may be a limited molt migration, or it may be a shift to a fall migration staging area. The extent and pattern of this emigration deserves further investigation if we are to understand the impact of the loss of small private wetlands.

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Growth rates and development of Redhead ducklings.—Variation in avian growth rates has been found to be related to adult body size (Ricklefs, Ibis 110:419–451, 1968), feeding ecology (Lack, Ecological Adaptations for Breeding in Birds, Methuen, London, England, 1968; Ricketts and Prince, Ornis. Scand. 12:120–124, 1981), predation pressure (Lack, 1968; Clark and Wilson, Quart. Rev. Biol. 56:253–277, 1981) and precocity of development

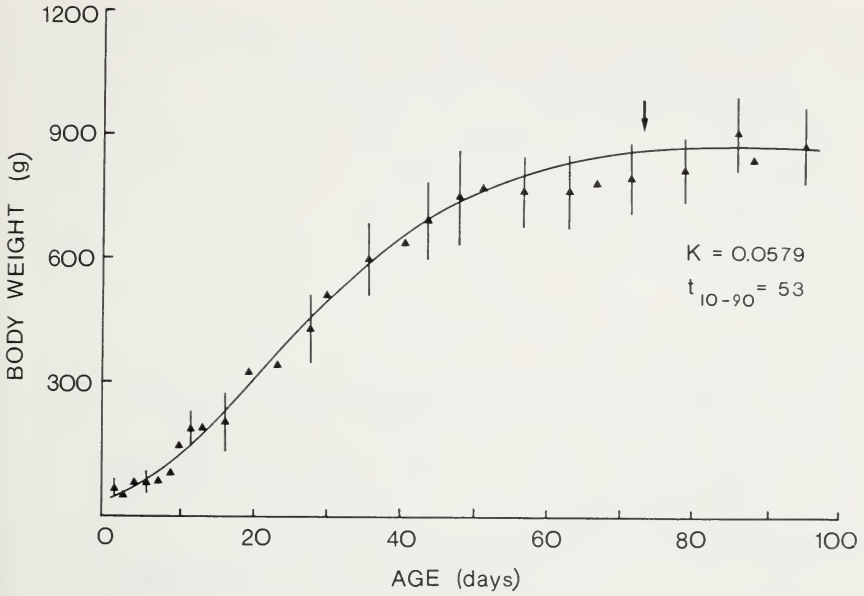

FIG. 1. Growth of Redhead ducklings (N = 11) raised in captivity. Individual points are means, and the arrow indicates the mean age at fledging. The curve was best fit by the Gompertz equation. Vertical bars are standard deviations.

(Ricklefs, Ibis 115:177–201, 1973; Biol. Rev. 54:269–290, 1979). Lightbody and Ankney (Auk 101:121–133, 1984) suggested that there also may be a seasonal influence on growth rate. Variation in patterns of growth is difficult to assess adequately unless there are sufficient, similarly collected and analyzed data. Ricklefs (1968, 1973) synthesized the results of many growth studies, but most were not directly comparable to one another owing to differences among the studies in methods of obtaining growth data (e.g., wild vs penned birds; if penned, by how they were reared; if wild, by how they were aged).

Ricklefs (Ecology 48:978–983, 1967) presented a simple graphical method for determining growth rate (K), asymptote (a), and the type of equation by which the data are best described (logistic, Gompertz, von Bertalanffy). Other methods (Richards, J. Exp. Bot. 10:290–300, 1959; Fendley and Brisbin, Proc. XIII Int. Congr. Game Biol. 337–350, 1977) produce estimates of K that differ from one another and from Ricklefs' estimate. The time required to grow from 10 to 90% of asymptotic size ($t_{10\text{-}90}$) is a less ambiguous value than K for comparing growth of body parts fitted to different forms of growth curves because it represents the linear part of the growth curve and is roughly comparable among the types of curve (Ricklefs 1967). Curves plotted as a function of the species' Growth Index (a time scale that makes the curves coincide along the abscissa; the growth index at time t is $G_t = [t - t_{50}]/[t_{50} - t_{10}]$ where t_{10} and t_{50} are the ages at 10 and 50% of asymptotic size) permit comparisons of relative growth of a body part (component) among species.

It is instructive to examine patterns of growth in closely related species, preferably intrageneric, so that a partial separation of environmental influences from phylogenetic differences can be achieved. Growth rates of waterfowl (Anatidae), particularly diving ducks (tribe

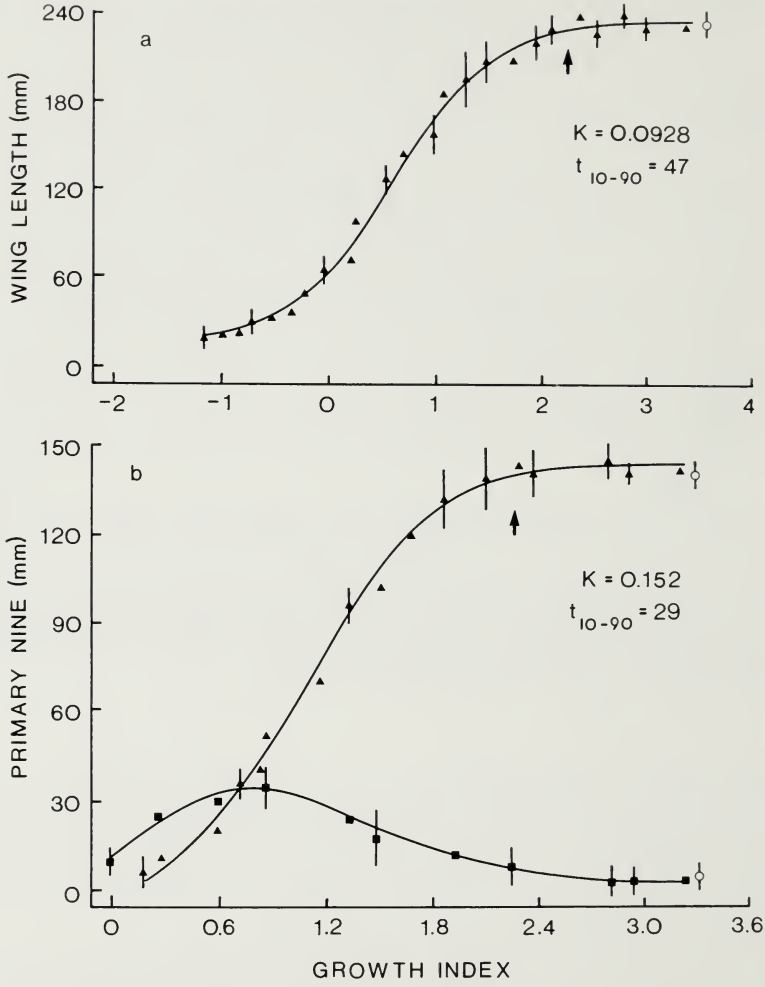

FIG. 2. Growth of (a) the wing and (b) the ninth primary shaft (squares) and feather excluding shaft (triangles) of Redhead ducklings (N = 11) raised in captivity. Solid points are mean values, and open circles are mean values at one year. The arrows indicate the age at fledging. Both curves were best fit by the Logistic equation. Vertical bars indicate standard deviations.

Aythyini), have not been investigated frequently. Herein I describe the pattern of growth and development of captive Redheads (*Aythya americana*) in the same manner as I described growth patterns of two other species of diving ducks, the Canvasback (*A. valisineria*) and the Lesser Scaup (*A. affinis*) (Lightbody and Ankney 1984). Redheads are intermediate in size between the larger Canvasback and the smaller Lesser Scaup, and they nest at the same

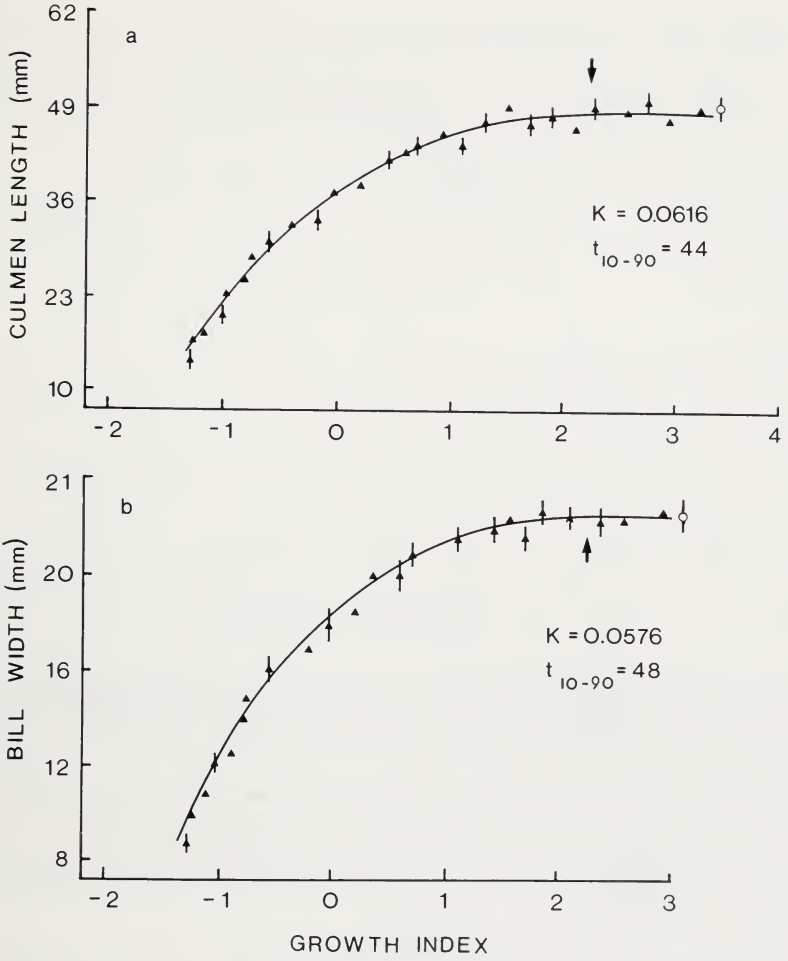

FIG. 3. Growth in (a) length and (b) width of the bill of Redhead ducklings (N = 11) raised in captivity. Solid points are mean values; open circle is the mean value at one year. The arrow indicates the age at fledging. Both curves were best described by the von Bertalanffy equation. Vertical bars indicate standard deviations.

time as Canvasbacks; thus a comparison of the growth rates of these three species is useful in investigating the seasonal influence of growth suggested by Lightbody and Ankney (1984). Growth curves of some body components (see below) are compared to values reported by Weller (Wilson Bull. 69:5–38, 1957) for Redheads, and growth rates are determined for each component using Ricklefs' (1967) method; growth rates for body components have not been reported previously for this species.

As Redheads commonly parasitize Canvasback nests, I was able to collect Redhead eggs

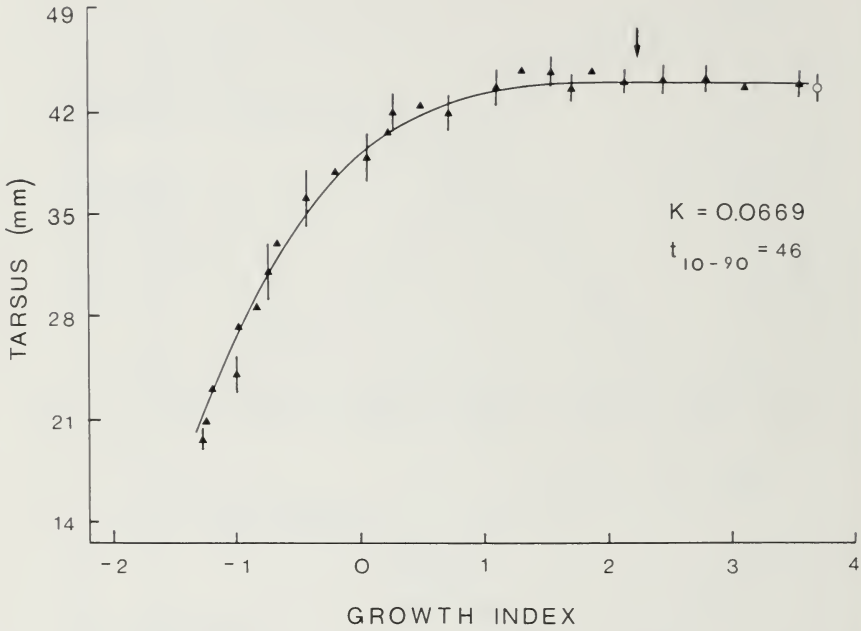

FIG. 4. Growth of the tarsus of Redhead ducklings (N = 11) raised in captivity. Solid points are means, and the open circle is the mean value at one year. The curve was best described by the von Bertalanffy equation. Vertical bars indicate standard deviations.

from parasitized nests (one egg per nest) while collecting Canvasback eggs near Minnedosa, Manitoba, during May 1981. Each Redhead egg probably came from a different female as parasitized nests were several miles apart. Eleven eggs were hatched in incubators, and the resulting seven males and four females were reared according to standard procedures (Ward and Batt, Propagation of Captive Waterfowl, Delta Waterfowl Res. Station and Wildl. Manage. Inst. Publ., Washington, D.C., 1973).

Measurements were made on the ducklings at hatching, every other day until they were two weeks old, and then every four days until they were several weeks past fledging, which occurred when the young were about 10 weeks old. Birds were considered fledged when the shafts of all primaries were firm and clear (Weller 1957). The ducks were measured again in June 1982 at one year of age. Weight, wing length, ninth primary shaft length and feather length excluding the shaft, tarsus, culmen length, and bill width were measured (see Lightbody and Ankney 1984 for details).

Growth curves were plotted for each component using the means for all ducklings, and (K) and $t_{10\text{-}90}$ were derived from each curve following Ricklefs' (1967) method. Growth curves were plotted vs Growth Index.

As there were no significant differences in size of males and females (t-tests at each week of age, $P > 0.05$) up to one week after fledging, data from both sexes were pooled for analyses. I did not calculate values for each duckling; only mean values were used for the analyses. The growth rate I calculated ($K = 0.058$) (Fig. 1) was higher than that which Ricklefs (1973) calculated using Weller's (1957) data ($K = 0.041$). Body weight is affected by many factors

(e.g., food quality, ambient temperature, activity level). Differences in these factors may make the growth rates variable, so the range of values in both studies may overlap. Ducklings fledged at 92.6% of the estimated asymptotic weight and reached that asymptote at day 85 (Fig. 1). A decline in weight was evident beginning two weeks before fledging. Similar declines have been reported for Mallards (*Anas platyrhynchos*) (Sugden et al., Can. J. Zool. 59:1567–1570, 1981; J. M. Rhymer, pers. comm.), Canvasbacks (Dzubin, J. Wildl. Manage. 23:279–290, 1959), Lesser Scaup (Sugden et al. 1981), and Redheads (Weller 1957); although Lightbody and Ankney (1984) found no such decrease for Canvasbacks or Lesser Scaup. Flight and muscle growth and development are energetically expensive, so it is not surprising that the birds lost weight at that time. That Lightbody and Ankney (1984) found no weight loss for Canvasbacks or Lesser Scaup may be due to lower levels of activity of individuals of these species compared to Redheads (pers. obs.).

Wing length increased rapidly and attained adult size at the time of fledging (Fig. 2a). Primaries emerged on day 28. The ninth primary grew rapidly, reaching adult length by the time the birds fledged (Fig. 2b). Primary shafts started to clear on day 54, and ducklings flew short distances over 1-m high dividers into the next section in the pen as early as day 63, when seven shafts were clear. Redheads seemed incapable of, or unwilling to attempt, sustained flight at that age, and they did not fly when tossed into the air. Ducks fledged on day 73 ± 2 [SD] (Fig. 1), which is near the upper end of the range of values reported by Smart (57–75 days, J. Wildl. Manage. 29:533–536, 1965) and Weller (56–73 days, 1957).

The bill grew faster in length than in width, and at the time of fledging, it had obtained adult length and width (Fig. 3), as reported by Weller (1957). The tarsus grew at a moderate rate (Fig. 4), yet reached adult size well before fledging. Weller (1957) found similar growth curves for these components. One-year-old birds had not grown since the time of fledging (Figs. 2–4).

Overall, body growth may be limited by tissue constraints (Ricklefs 1973, 1979), but the pattern of development and growth rates of various components may depend upon the allocation of energy at the organism level. Pattern of development, growth, and fledging age of Redheads were similar to those of Canvasbacks (Lightbody and Ankney 1984), which are exposed to the same environmental conditions in the wild (e.g., temperature, daylength, habitat characteristics). Growth rate is usually related inversely to body size within a phylogenetic family (Ricklefs 1968), and because Redheads are smaller than Canvasbacks, they should grow faster. That they do not, suggests that either Redheads grew relatively slower or that Canvasbacks grew relatively faster than expected, or both. Redheads fledged older and grew slower in all components than did Lesser Scaup (Lightbody and Ankney 1984), which hatch later in the season under different environmental conditions. This was true even after accounting for differences in body size. Thus, there may be a seasonal influence on growth rates.

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Kin cannibalism in the Purple Gallinule.—Kin cannibalism, the killing and consumption of closely related conspecifics, is rare in birds. Among some species of raptors, an older chick may kill its younger sibling (Stinson, Evolution 33:1219–1225, 1979) and occasionally will consume the dead sibling (Ingram, Auk 76:218–226, 1959; Pilz and Siebert, Auk 95: 584–585, 1978). There are few documented cases of parents cannibalizing their own young. Piñon Jays (*Gymnorhinus cyanocephalus*) sometimes kill and eat their chicks (Balda and Bateman, Condor 78:562–564, 1976), and Herring Gulls (*Larus argentatus*) may eat their eggs and chicks (Chardine and Morris, Wilson Bull. 95:477–478, 1983). Kin cannibalism is attributed to food deprivation (Ingram 1959; Balda and Bateman 1976; Bechard, Wilson Bull. 95:477–478, 1983), or unusual and aberrant chick behavior (Siegel-Causey, Condor 82:101, 1980).

During a 17-month study of Purple Gallinule (*Porphyrula martinica*) breeding behavior at the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) near Turrialba, Costa Rica, I color-banded 80 birds, observed 36 nests, and followed the development of 120 chicks. Members of mated pairs took turns incubating the eggs (usually 4), which hatched asynchronously over 3–4 days. Normally, chicks remained in the nest until all eggs hatched. After the chicks left the egg-nest they were brooded in a separate nursery-nest, which was within 5 m of the egg-nest.

The female of a marked pair finished laying a clutch of 4 eggs approximately 4 m from my observation blind on 3 August 1981. On the morning of 25 August at 07:35 the male was brooding a newly hatched chick in a nursery-nest less than one m from the egg nest. None of the other eggs had hatched. The female was not in sight. At 07:55 the female came to the male, fed him an insect and left. She returned at 08:25 to feed the male another insect and then settled on the egg-nest. The male left the nursery-nest at 08:30 and pulled the chick after him. Twice, the chick crawled back into the nursery nest and the male pulled it out. The male preened the chick and began pecking at it at 08:40. The chick grew limp within one min, and the male tore off pieces of its body and ate them. At 08:46, after consuming approximately five bites of the chick, the male walked 6 m to the northeast and began feeding. At 09:05 the female left the egg-nest and the male settled on the eggs.

The male was incubating when I departed at 09:40. I inspected the nursery-nest at 10:30 but could not find the remains of the chick. The egg-nest contained 3 eggs. Two chicks hatched over the next 2 days; one lived for one day and the other lived for one month. Both chicks disappeared, and the causes of death were unknown. Prior to this episode the pair had raised 2 broods (totaling 6 chicks) successfully. During the next nine months the pair raised 3 more broods, totaling 8 chicks. The pair did not exhibit any other unusual behavior throughout the study period. The events described constitute the only act of cannibalism that was seen during the study.

The male may have killed and eaten the chick for several reasons: (1) he was food deprived, (2) the chick was not his, (3) the chick was malformed, or (4) the chick behaved in an unusual manner. The evidence concerning these possibilities follows: First, the male did not appear to be hungry. The weather had been mild, food was abundant, and the male was fed by his mate at least twice just before his act of cannibalism. Second, all evidence suggests that the chick came from the pair's egg-nest. At the time no other gallinule family on the pond had young chicks or a clutch of eggs about to hatch. I did not observe another male copulating with the female, and I never saw cuckoldry among any of the gallinules during my study. I can not rule out, however, the possibility that the male was cuckolded without my witnessing the event. Third, the chick looked healthy and well-formed. Fourth, it was

unusual for the chick to leave the egg-nest when it did. No other chick had been observed outside the egg-nest before the majority of eggs (at least 3) had hatched. Nothing in the parents' behavior appeared to have forced the chick from the nest. Perhaps the male's physiological state at the time the chick left the nest was not conducive to responding appropriately (i.e., brooding) to the presence of chicks (Beer, Behaviour 26:190–214, 1966). He may have had conflicting tendencies to incubate the eggs and to brood the chick, or simply was not motivated to brood. Why he ate the chick is not known.

The staff at the Centro Agronómico Tropical de Investigación y Enseñanza kindly allowed me to use their facilities. K. L. Bildstein, R. L. Hutto, D. A. Jenni, A. F. Poole, and an anonymous reviewer provided helpful comments on earlier drafts of the manuscript. My research was supported by NSF Grant DEB-8016658, the Chapman Memorial Fund, and the Explorer's Club.—Laurie A. Hunter, *Dept. Zoology, Univ. Montana, Missoula, Montana 59812.* *Accepted 12 Apr. 1985.*

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Influence of various land uses on windbreak selection by nesting Mississippi Kites.—Contemporary land-use practices have dramatically altered breeding habitats of birds of prey (Cramp, pp. 9–11 *in* World Conf. Birds of Prey, R. D. Chancellor, ed., ICPB, London, England, 1977). Some land uses appear to influence strongly both the nesting activity (White, Trans. North Am. Wildl. Nat. Resour. Conf. 39:301–312, 1974) and abundance (Olendorff and Stoddart, pp. 44–48 *in* Management of Raptors, F. N. Hamerstrom, B. E. Harrel, and R. R. Olendorff, eds., Proc. Conf. Raptor Conserv. Tech., Raptor Rep. 2, Fort Collins, Colorado, 1974) of raptors.

The Mississippi Kite (*Ictinia mississippiensis*) is a locally common raptor of the south-central plains of North America. In the prairie grasslands of western Oklahoma and southwestern Kansas, kites commonly nest in tree plantings designed as windbreaks, irrespective of windbreak width, age, or tree species composition (Parker, Ph.D. Diss., Univ. Kansas, Lawrence, Kansas, 1974; Love and Knopf, Proc. Ann. Meet. For. Comm. Great Plains Agric. Counc. 30:69–77, 1978). Much of the potential nesting habitat within this region, however, is not used by kites (Parker and Ogden, Am. Birds 33:119–129, 1979). In this paper, we assess the potential influence of various land-use practices on windbreak selection by nesting Mississippi Kites.

Study area and methods.—The study areas were located in Clark and Meade counties, southwestern Kansas; and Ellis, Harper, and Roger Mills counties, northwestern Oklahoma. The region is classified as bluestem–grama prairie (*Andropogon–Bouteloua*) and grama–buffalo grass plains (*Bouteloua–Buchloe*) by Kuchler (Potential Vegetation of the Conterminous United States, Am. Geogr. Soc., New York, New York, 1964). Agricultural lands frequently contained plantings of wheat, sorghum, and, occasionally, alfalfa. Native deciduous vegetation generally was limited to narrow belts of riparian woodland dominated by cottonwood (*Populus deltoides*), and aggregations of shinnery oak (*Quercus havardii*). Tree species commonly present in planted windbreaks were black locust (*Robinia pseudoacacia*), eastern red cedar (*Juniperus virginiana*), elm (*Ulmus* spp.), green ash (*Fraxinus pennsylvanica*), osage orange (*Maclura pomifera*), and Russian mulberry (*Morus alba*). Conifers usually comprised the sides of tree plantings that received the prevailing winds.

Systematic searches for kite nests were conducted at 89 windbreaks during June and July of 1977 and 1978. Windbreaks were classified as unused, with 1–2 kite nests, or with >2 nests.

TABLE 1
DESCRIPTIONS OF LAND-USE CATEGORIES USED IN THE STUDY

Land-use category	Description
Wheat fields	Green harvestable stubble or mulch.
Cropland	Sorghum and small grains other than wheat.
Irrigated cropland	Fields of alfalfa; rarely wheat or cotton.
Sage	Dominated by sand-sagebrush, including shinnery.
Degenerating grassland	Overgrazed and eroded sand-sagebrush and shortgrass plains.
Grassland	Prairie and pasture not degenerating.
Bottomland forest	Riparian woodland.
Upland forest	Including other windbreaks.
Windbreak measured	
Water	Permanent bodies of water.
Homesteads	
Roads and rights-of-way	
Other land uses	Includes petroleum drilling operations, golf courses, etc.

Land-use practices were quantified from aerial photographs (scale 1:20,000) for circular areas 2 km from the middle of a given windbreak. The centers were established arbitrarily to standardize the analysis for unused windbreaks and those used by >1 pair of kites. Land was classified in 13 categories according to vegetation cover (Table 1). Kites may feed at a distance from their nests (Skinner, Auk 79:273–274, 1962); to accomodate the potential influence of distance from the windbreak, the amount of each cover-type was measured for two concentric zones from 0 to 1 km (zone 1) and 1 to 2 km (zone 2).

The area of windbreak in zone 2 was invariate; this variable was eliminated. Thus, 25 variables were generated from the 13 cover-types and two zones. In addition, six variables identifying characteristics of the windbreak itself were measured. These included the length of the windbreak, its width, the number of tree rows, the number of snags, and two variables measuring the distance to a road from the closest point to the road and from the center of the windbreak.

Thirty-six windbreaks were used in the analysis. We chose windbreaks of different classes (i.e., unused, with 1–2 nests, and with >2 nests) that were at least 4 km apart in any year to avoid overlaps in land area.

The 31 variables were standardized (Y = 0.0, SD = 1.0) and the matrix of variables and windbreaks subjected to principal components analysis (PCA) using NT-SYS (Numerical Taxonomy System; Rohlf et al., NT-SYS. Numerical Taxonomy System of Multivariate Statistical Programs, State Univ. New York, Stony Brook, New York, 1979). PCA draws new axes through the data orthogonal (and thus uncorrelated) to each other and ordered on the basis of the amount of total variation explained (Morrison, Multivariate Statistical Methods, McGraw-Hill Book Co., New York, New York, 1976; Neff and Marcus, A Survey of Multivariate Methods for Systematics, Am. Mus. Nat. Hist., New York, New York, 1980); the first principal components axis would account for the most variation, etc. Components axes were then used as new variables, each component representing a gradient formed by the combination of original variables with high loadings (i.e., correlations) onto it.

The values of the windbreaks on the PCA axes were subjected to analysis of variance

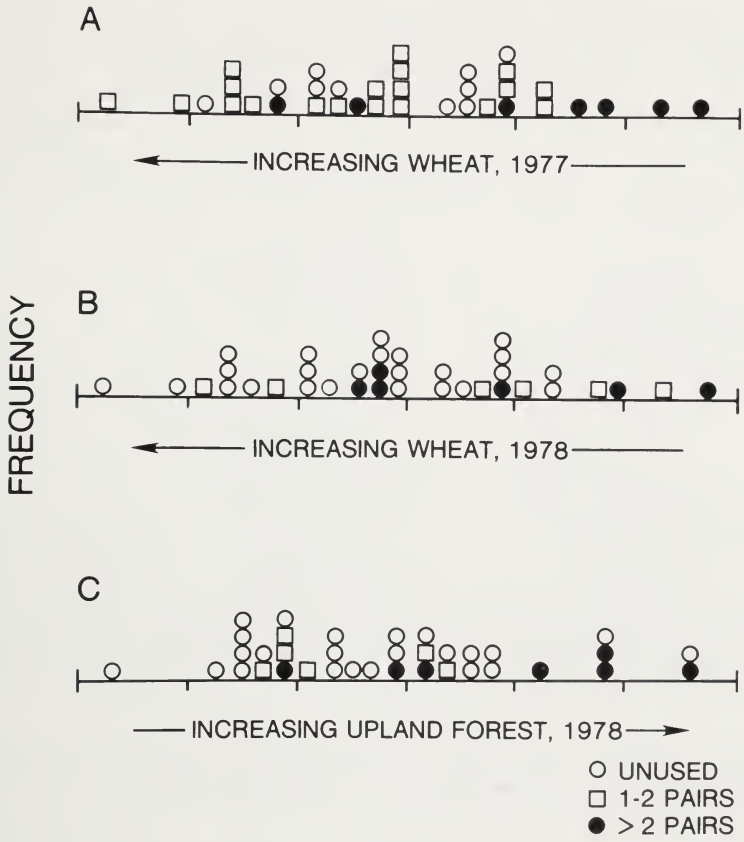

FIG. 1. Projections of windbreaks onto principal component 1 for 1977 (A) and 1978 (B), and component 3 for 1978 (C). See Table 2 for more complete descriptions of these axes. Use is for pairs of nesting Mississippi Kites.

(ANOVA) and Duncan's multiple range test using SAS package programs (Helwig and Council, eds., SAS User's Guide, SAS Institute, Cary, North Carolina, 1979), where the treatments or groups are the kite occupancy classes. Bartlett's Test (Sokal and Rohlf, Biometry, W. H. Freeman and Co., San Francisco, California, 1969) was used to determine if the homogeneity of variance assumption was met for the groups on each components axis.

The new variables were derived independently of the kite occupancy classes; however, if the presence of these groups increases the variation, these groups should contribute most to the first principal component. These groups would then contribute least to the variation of the second component, because it is orthogonal and uncorrelated with the first. Thus, the analysis presented here should extract the gradient from the data on which kites occur nonrandomly, and verify if such a result is likely to be significant biologically.

Results.—The number of active kite nests differed greatly between years. Five of 36

TABLE 2

DESCRIPTION OF THE FIRST THREE PRINCIPAL COMPONENTS AXES FOR 1977 AND 1978[a]

Principal component	1977	1978	% Variation explained 1977	% Variation explained 1978
1	D[b] Wheat	D Wheat	17.7	17.5
	D Rights-of-way	I Windbreak		
	I Sage	D Rights-of-way		
	I Windbreak	D Cropland (zone 1)		
	D Homesteads	I Sage		
	I Grassland (zone 1)	D Homesteads		
	D Cropland (zone 2)			
2	I Water (zone 2)	I Water (zone 2)	13.1	13.0
	D Distance to roads	D Degenerating grassland		
	D Degenerating grassland	I Bottomland forest		
	I Bottomland forest	I Grassland (zone 2)		
	I Grassland (zone 2)	D Distance to roads		
3	I Upland forest	I Upland forest	9.3	7.8
	I Water (zone 1)	I Water (zone 1)		
	I Windbreak	D Other land-uses		

[a] Tables giving the loadings of vegetation cover variables are available from the authors.

[b] Variables are listed in decreasing order of importance for each component. See Table 1 and text for descriptions of variables. D = Decreasing; I = Increasing.

windbreaks (14%) had more kite nests in 1978 than in 1977, and 21 (55%) had fewer; 27 of 36 windbreaks (75%) were used by at least one pair of kites in 1977, but only 13 (36%) were used in 1978. Six windbreaks (17%) were not used in either year; two (6%) were used by 1–2 nesting kite pairs both years; and five (14%) were used by >2 kite pairs both years.

A summary of the most important variables for the first three components in each year is given in Table 2. The results of the ANOVA's for the 1977 data indicate a highly significant relationship for component 1 ($F = 4.99$, $P < 0.01$), but not for component 2 ($F = 0.57$, $P > 0.57$). Land surrounding windbreaks with high values for component 1 is characterized most strongly by less wheat, and also by more grassland in zone 1, more sage, and fewer homesteads, roads, and rights-of-way (Table 2). Windbreaks with the highest values on component 1 were used heavily by kites (Fig. 1A) with 7, 8, and 9 nests per windbreak. Windbreaks used by three or more pairs of nesting kites were significantly different from the other windbreaks on component 1 (Multiple range test, $P < 0.05$), but windbreaks used by 1–2 nesting kite pairs and unused windbreaks did not differ from each other significantly ($P > 0.05$).

Whereas six of the seven windbreaks with the lowest values on component 1 were used for nesting by at least one pair of kites, only one of these seven was used in 1978 (Fig. 1B). Thus, kites generally did not use the areas with the highest wheat values in 1978. The three windbreaks with high values on component 1 had 2, 4, and 10 kite nests. Component 1 for the 1978 data was similar to that in 1977 (Table 2); however, the ANOVA for the first component was not significant ($F = 2.05$, $P > 0.14$), nor was the ANOVA for the second component ($F = 0.41$, $P > 0.67$). The ANOVA for the third component in the 1978 data was significant ($F = 3.76$, $P < 0.05$); a multiple range test again separated the heavily used

windbreaks from the other windbreaks on this component ($P > 0.05$). Heavily used windbreaks were at the upper values of component 3 (Fig. 1C); the lands surrounding these windbreaks were characterized by more upland forest (including windbreaks), more surface area of water, and less of the other land-use category (Table 1).

Discussion.—Kites tended to use the larger windbreaks that were surrounded by more native vegetation with less agricultural land, and with fewer nearby homesteads and roads than the overall sample. Kalla and Alsop (Am. Birds 37:146–149, 1983) also noted an avoidance of "farmland" (much of which was in soybean production) by kites in Tennessee. Kites, however, are frequently found in towns with much human activity, and appear to be very tolerant of human disturbance (Parker 1974, Parker and Ogden 1979).

Parker and Ogden (1979) argued that kite populations in the Great Plains have benefited from an increase in prey populations, primarily Orthopterans, caused by irrigation and overgrazing. Wheat, however, is a dryland crop which would not enhance prey populations, making lands with substantial wheat marginally suitable for kites. Kites foraging on large insects can be opportunistic (Skinner 1962, Parker 1974), and could depend on ephemerally abundant prey from a variety of habitats; however, wheat cropland would have limited capacity for such foraging opportunities.

High occupancy rate of windbreaks in preferred areas may induce some kites to use windbreaks surrounded by marginal or deficient habitat. Lands surrounding most windbreaks were planted primarily in wheat. This may explain the general scatter of points for the unused windbreaks and windbreaks used by 1–2 pairs of nesting kites, and the lack of significant differences between classes on component 1 in the 1978 data (Fig. 1B).

The mosaic distribution of land-use types also may influence windbreak use by nesting kites. Glinski and Ohmart (Condor 85:200–207, 1983) argued that vegetation patchiness enhanced foraging success, and thus reproduction, in kites. The birds they studied in Arizona foraged in a patchy arrangement of cottonwood and salt cedar (*Tamarix chinensis*). Kites were common in many towns in our study area (Parker 1974) and in the cross-timbers scrubland of west-central Oklahoma (pers. obs.); both present a mosaic patchwork of open and treed areas. Windbreaks themselves can create a patchy mosaic. In addition to providing nesting sites and potential habitat for prey, their arrangement in patches with other nonwheat habitat types may enhance foraging opportunities for kites by creating "edge," and by locally reducing wind speeds.

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Species-area relationship of birds on small islands at Isle Royale, Michigan.—Most studies of avian biogeography have described species distribution patterns across huge archipelagoes (Simberloff, pp. 411–455 *in* Perspectives in Ornithology, A. H. Brush and G. A. Clark, Jr., eds., Cambridge Univ. Press, Cambridge, England, 1983). In comparison, bird populations on groups of small islands close to one another and to the species source pool have received little attention (but see Galli et al., Auk 93:356–364, 1976; Morse, Condor 79:399–412, 1977; Rusterholz and Howe, Evolution 33:468–477, 1979). The factors that influence species composition on such islands are likely to be quite different from those considered in the classic theoretical models of island biogeography (MacArthur and Wilson, Island Biogeography, Princeton Univ. Press, Princeton, New Jersey, 1967). Very small islands are mostly inhabited by migrant birds that "go extinct" and "recolonize" each year, and the proximity of islands enables birds to defend territories that include more than one island.

This paper presents data on the number of bird species on 36 small islands at the northeast end of Isle Royale Wilderness National Park, Michigan. The results show that the use of multiple islands by breeding birds complicates the interpretation of species-area data from very small islands.

Methods.—The 36 islands, ranging from 3 m^2 to 20.6 ha, are all within 1.5 km of Isle Royale, which is as close as 18 km from the north shore of Lake Superior. Isle Royale contains essentially all breeding birds present on the adjacent Canadian mainland (Jordon and Shelton, Wildlife of Isle Royale, Isle Royale Nat. Hist. Assoc., Houghton, Michigan, 1982), and the water between islands does not present a barrier to regular avian colonization. Dominant trees on these islands include white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*). Two censuses of the breeding bird populations on each island were made between 11 June and 12 July 1983. Because all islands are narrowly elongated along a NE–SW axis, bird populations could be counted accurately by walking the length of the island, and census duration was roughly proportional to island area. A species was considered present if it was recorded on at least one census; the number of males was estimated by averaging the results of the two censuses. By sampling each island on only two occasions, I may have generated an incomplete record of species occurrences by overlooking inconspicuous species, and I may have overestimated birds that traveled between islands.

Species-area data were fitted by the power function, $S = cA^z$, where S is number of species + 1 (several islands had zero species), A is island area (ha; excluding the exposed, rocky shores of the outermost islands), and the parameters c and z are estimated by the intercept and slope of the regression of log-species on log-area. The correlation coefficient, used to assess the fit of the model, was calculated by a second regression of species number on area raised to the power z obtained from the original log-log regression (Martin, Am. Nat. 118:823–837, 1981).

Results and discussion.—The number of breeding species increases as a function of island area throughout the range of island sizes present in the study (Table 1). The log-log regression equation of species richness on area explains most of the variance among islands in species richness ($r = 0.953$, $P < 0.0001$; $z = 0.281 \pm 0.063$ [95% CI], $c = 4.33 \pm 1.17$). After excluding the two smallest islands (3 m^2 and 10 m^2), which are well below the minimum size necessary to support breeding birds, the slope and intercept increase to $z = 0.341 \pm 0.063$ and $c = 4.46 \pm 1.16$, but the fit of the power function remains unaltered ($r = 0.957$, $P < 0.0001$).

Table 1

Estimated Number of Males of the 10 Most Common Species on 36 Islands

Island	Size (ha)	No. of males present									
		SS[a]	YR	NA	MA	WW	WT	AR	ST	BL	RN
Hidden Rock	0.0003	0	0	0	0	0	0	0	0	0	0
Split Rock	0.001	0	0	0	0	0	0	0	0	0	0
Storm	0.02	0.5	0	0	0	0	0	0	0	0	0
Short	0.03	0	0	0	0	0	0	0	0	0	0
Kemmer	0.03	0.5	0.5	0	0	0	0	0	0	0	0
East Split	0.05	1.0	0	0	0	0	0	0	0	0	0
First	0.05	0.5	0.5	0	0	0	0	0	0	0	0
West Split	0.08	1.0	0	0	0	0	0	0	0	0	0
Emerson	0.09	0.5	0.5	0	0	0	0	0	0	0	0
Musselman	0.10	1.0	0	0	0	0	0	0	0	0	0
Middle Tobin	0.11	0.5	0.5	0	0	0	0	0	0	0	0
Green	0.15	1.0	0.5	0	0	0	0	0	0	0	0
West Tobin	0.17	1.0	1.0	0	0	0	0	0	0	0	0
Hidden	0.18	1.0	0.5	0	0	0	0	0	0	0	0
Gem	0.19	1.0	0.5	0	0	0	0	0	0	0	0
Howe	0.22	0.5	0	0	0	0	0	0	0	0	0
Lion	0.34	2.0	0	0	0	0	0	0	0	0	0
Porter Islet	0.35	1.0	0.5	0	0	0	0	0	0	0	0
Baily	0.36	1.0	0	0	0	0	0	0	0	0	0
East Tobin	0.37	1.0	1.0	0.5	0	0	0	0	0	0	0
Third	0.40	1.0	1.0	0	0	0	0	0	0	0	0
Flag	0.49	2.5	1.0	0	0	0	0	0	0	0	0
Savage	0.71	0	1.0	0	0.5	1.0	0	0	0	0	0
Smith	0.88	1.0	1.0	0	0	0	0	0	0	0	0
Merritt I	0.93	0.5	1.0	0.5	0.5	0	0.5	0	0	0	0
Gale	1.01	1.0	1.5	0.5	1.0	0	1.0	0.5	0	0	0
Second	1.20	2.0	1.0	0	1.0	0	0	0.5	0	0	0
Merritt II	1.43	2.0	1.0	0	0.5	0	0.5	1.5	0	0	0
Newman	1.69	1.0	2.0	1.0	0.5	0	0	0	0.5	0	0
North Gov't.	1.84	3.0	1.0	1.0	0	0	0	1.0	0.5	0	0
Boys	2.87	1.0	2.0	1.0	1.0	1.0	2.0	1.0	0	0	0
South Gov't.	3.73	4.0	4.5	0.5	0	1.0	0	1.0	0.5	0	0
Long	3.97	2.5	2.0	0.5	0	1.0	0.5	0	0	0.5	0
Minong	7.81	1.0	2.0	2.0	1.5	0.5	1.5	1.0	1.0	0	0
Edwards	10.47	3.0	6.0	5.0	2.0	2.0	0	2.0	1.0	1.0	2.0
Porter	20.58	4.0	12.0	9.0	8.5	3.0	7.0	1.0	3.0	0.5	1.0

[a] Abbreviations of species are as follows: SS = Song Sparrow (*Melospiza melodia*), YR = Yellow-rumped Warbler (*Dendroica coronata*), NA = Nashville Warbler (*Vermivora ruficapilla*), MA = Magnolia Warbler (*D. magnolia*), WW = Winter Wren (*Troglodytes troglodytes*), WT = White-throated Sparrow (*Zonotrichia albicollis*), AR = American Redstart (*Setophaga ruticilla*), ST = Swainson's Thrush (*Catharus ustulatus*), BL = Blackburnian Warbler (*D. fusca*), and RN = Red-breasted Nuthatch (*Sitta canadensis*).

TABLE 2

COMPARISON OF SIZE (HA) OF THE SMALLEST ISLAND OCCUPIED AT ISLE ROYALE AND AVERAGE TERRITORY SIZE IN A LARGE POPULATION IN MAINE

Species	Smallest island occupied at Isle Royale	Mean (N) territory size in Maine[a]	Smallest island expressed as % of mean territory size in Maine
Song Sparrow	0.02	0.26 (24)	7.7
Yellow-rumped Warbler	0.03	0.81 (17)	3.7
Winter Wren	0.71	3.64 (2)	19.5
Magnolia Warbler	0.71	0.72 (9)	98.6
White-throated Sparrow	0.93	0.62 (18)	150.0

[a] Data for mainland population in Maine from Morse (1977: Table 5).

The biological significance of the parameters c and z of the species-area curve has been considered for some time (MacArthur and Wilson 1967; Connor and McCoy, Am. Nat. 113:791–833, 1979; Gould, Am. Nat. 144:335–343, 1979; Martin 1981). The coefficient c is the projected number of species on an island of unit area (one ha, in this study), and is useful for comparisons of species diversity among sets of archipelagoes with equal z's (Gould 1979). According to my analysis, an average of 4.3–4.5 breeding species should occur on a one-ha island at Isle Royale. Maximum increases in species diversity with incremental increases in area (maximum z values) seem to occur in groups of small islands. The z calculated for the islands in this study is lower than the values for six groups of islands of similar size reviewed by Martin (1981, $z = 0.388–0.542$), probably because my smallest islands were only barely large enough to support breeding birds, so that males on these islands had multiple islands in their territories. Including only islands at least 0.1 ha in the regression gives an estimate within the range of slopes summarized by Martin ($z = 0.392 \pm 0.108$, $N = 26$, $r = 0.963$, $P < 0.0001$).

My results permit estimation of the minimum area requirements for several common species of birds at Isle Royale. Song Sparrows appear on a 0.02 ha island, but do not regularly occur below roughly 0.05 ha. Yellow-rumped Warblers breed on the majority of islands greater than 0.10 ha. Nashville and Magnolia warblers do not breed on islands smaller than 0.4–0.7 ha, and Winter Wrens and White-throated Sparrows require approximately 0.7–0.9 ha. These smallest-island records should be accepted with caution, however, as these birds may use more than one island. For example, it is probably not reasonable to suppose that a pair of Song Sparrows confined their breeding activities to an island only 0.02 ha in size (Storm Island, Table 1). In fact, I made a number of observations of Song Sparrows and Yellow-rumped Warblers traveling between adjacent islands.

These results support the observation that some birds occupy smaller areas on islands than in mainland habitats (Yeaton and Cody, Theor. Popul. Biol. 5:42–58, 1974; Morse 1977). Morse (1977) compared mainland and island territory sizes of eight passerines on the coast of Maine and concluded that Song Sparrows, Yellow-rumped Warblers, and Northern Parulas (*Parula americana*) defended smaller territories on islands because of the absence of competitors. Five of Morse's (1977) species also occur in my study area (Table 2). At Isle Royale, the smallest islands occupied by Song Sparrows, Yellow-rumped Warblers, and Winter Wrens are 5–27 times smaller than the average territory sizes of these species in Morse's (1977) mainland populations. Magnolia Warblers and White-throated Sparrows

occupy areas of similar size on islands at Isle Royale and on the mainland in Maine (Table 2). Although these data are consistent with the hypothesis that certain species experience competitive release on islands at Isle Royale, they may also reflect the use of multiple islands by breeding males. Concurrent use of several islands would cause underestimation of area requirements, and might create the appearance of competitive release. Thus, studies of competitive release on archipelagoes of very small islands should include detailed observations of marked birds to determine individual patterns of island use.

Acknowledgments.—I wish to thank the Edwards family for enabling me to stay at Prospect Camp on Edwards Island during this study. Other support, equipment, and ideas were provided by H. W. Art, J. Edwards, W. T. Fox, and D. C. Smith. Referees T. E. Martin and J. M. Wunderle made helpful suggestions on the manuscript. Computing funds were made available by the Dept. Zoology, Duke Univ.—Joseph Van Buskirk, *Dept. Zoology, Duke Univ., Durham, North Carolina 27706.* *Accepted 3 Apr. 1985.*

Wilson Bull., 97(4), 1985, pp. 569–571

Avoidance of acoustic interference by Ovenbirds.—Two birds singing at the same time may mask each others' signals. In order to have their signals heard, birds should actively avoid both intraspecific and interspecific interference through temporal changes in the delivery of advertisement songs (Ficken et al., Science 183:762–763, 1974; Wasserman, Anim. Behav. 25:949–952, 1977), although experimental evidence is scarce (Schroeder and Wiley, Auk 100:414–423, 1983). Here, we report on the use of playbacks to investigate whether Ovenbirds (*Seiurus aurocapillus*) actively avoid intraspecific acoustic overlap. Lein (Wilson Bull. 93:21–41, 1981) has previously suggested that intraspecific avoidance occurs in this species.

The study site, at the University of Wisconsin–Milwaukee Field Station, Saukville, Ozaukee County, Wisconsin, was in an original growth, upland beech-maple forest. The playback tape consisted of 50 Ovenbird songs played at randomly determined intervals (6–48 sec) over a 12-min period. The response of the Ovenbirds was recorded with a Sennheiser MKH 104 omnidirectional condenser microphone connected to a Nagra III tape recorder placed 3 m from the speaker and 1.5 m off the ground. Recordings were made on five days (one experiment per day, with a different Ovenbird each day) between 15 June and 2 July 1968. All five Ovenbirds were color-banded. The Ovenbirds were in the nestling period of the nesting cycle during the study.

To determine the relative timing of songs, the tapes were analyzed using a Bruel and Kjaer 2305 graphic level recorder with a 2000 Hz high pass filter. The length of each song and the interval between songs were then measured. The predicted number of Ovenbird songs begun during a stimulus song is:

$$F = p(s)f$$

where f is the total number of nonstimulus songs and p(s) is the portion of recording time during which the stimulus tape was playing (Ficken et al. 1974). For this study p(s) equals 0.135.

A replicated goodness of fit test (G-statistic) was used for the statistical analysis (Sokal and Rohlf, Biometry, W. H. Freeman, San Francisco, California, 1981). This test permitted comparison of observed and expected values for each individual replicate as well as for the pooled results. In addition, a test of the heterogeneity of the ratios of the replicates was performed.

TABLE 1
OBSERVED AND EXPECTED NUMBERS OF OVERLAPS

Individual	Total number of songs	Observed overlaps	Expected overlaps	G	*P*
1	62	3	8.3	5.001	<0.05
2	66	4	8.9	3.850	<0.05
3	52	1	7.0	8.875	<0.005
4	60	1	8.1	10.946	<0.001
5	11	1	1.5	0.215	>0.05
Tests		df		G	*P*
Pooled		1		25.760	<0.001
Heterogeneity		4		3.094	>0.05
Total		5		28.854	<0.001

Ovenbirds should rarely mask stimulus songs if they are avoiding interference. During 251 songs the Ovenbirds overlapped the stimulus song only 10 times. The observed number of overlaps was significantly less than the expected number for the pooled sample and for four of the five replicates (Table 1). The test of heterogeneity was not significant, indicating there was little variation among individuals in overlap avoidance.

One way for Ovenbirds to avoid song interference would be to sing during the other individual's refractory period (the silent period following a song). In support of this hypothesis a greater percentage of Ovenbird song occurred during the first tenth of the silent interval between stimulus songs than would be predicted by chance for four of the replicates and for the pooled sample (Table 2). Once again there was little variation among individuals.

Experimental evidence from this study indicates Ovenbirds avoid intraspecific acoustic interference. Schroeder and Wiley (1983) also indicated male Tufted Titmice (*Parus bicolor*)

TABLE 2
PERCENT OF SONGS OCCURRING IN THE FIRST TENTH OF THE SILENT PERIOD BETWEEN STIMULUS SONGS

Individual	Observed	Expected	G	*P*
1	33.3%	10.0%	14.490	<0.001
2	34.4%	10.0%	13.899	<0.001
3	15.4%	10.0%	0.732	>0.05
4	34.4%	10.0%	13.899	<0.001
5	66.7%	10.0%	11.204	<0.001
Tests		df	G	*P*
Pooled		1	47.252	<0.001
Heterogeneity		4	6.971	>0.05
Total		5	54.223	<0.001

seldom overlapped songs, especially during playback experiments, although they provided no actual data or results of statistical tests. In addition, Wasserman's (1978) and Todt's (Z. Tierpsychol. 57:73–93, 1981) descriptive studies show that White-throated Sparrows (*Zonotrichia albicollis*) and European Blackbirds (*Turdus merula*) avoid intraspecific masking. Ovenbirds at least partially avoid masking by singing immediately after hearing conspecifics. This response could be the result of direct selection for overlap avoidance or the result of individuals answering the stimulus of a singing conspecific. Unlike the results Hultsch and Todt (Behav. Ecol. Sociobiol. 11:253–260, 1982) obtained for Nightingales (*Luscinia megarhynchos*), there was no evidence for individual variation among Ovenbirds in the tendency to avoid overlap. These results demonstrate the influence that singing conspecifics may have on the temporal patterning of song.

Acknowledgments.—We thank M. S. Ficken, L. Bunkfeldt-Popp, D. B. McNair, and R. Lein for their criticisms of the manuscript. C. Weise color-banded the birds. This is contribution no. 67 of the University of Wisconsin–Milwaukee Field Station.—Robert W. Ficken, James W. Popp, *Dept. Biol. Sci., Univ. Wisconsin–Milwaukee, Milwaukee, Wisconsin 53201,* and Paul E. Matthiae, *Field Station, Univ. Wisconsin–Milwaukee, Saukville, Wisconsin 53080.* (Present address PEM: *Bureau of Endangered Resources, Wisconsin Dept. Natural Resources, Madison, Wisconsin 53707.*) *Accepted 15 Apr. 1985.*

Wilson Bull., 97(4), 1985, p. 571

Gila Woodpecker stores acorns.—The Gila Woodpecker (*Melanerpes uropygialis*) has not been observed to store food, although close relatives, such as the Red-bellied Woodpecker (*M. carolinus*), are known to do so (Roberts, Am. Nat. 114:418–438, 1979; Short, Woodpeckers of the World, Delaware Mus. Nat. Hist. Monogr., 4, 1982). On 26 December 1984, near the main library at the University of Arizona, Tucson, Arizona, we watched a male Gila Woodpecker picking acorns from oaks (*Quercus* sp.), flying with them to a group of palm trees (*Washingtonia* sp., *Phoenix* sp.) about 75 m away, and storing them among the fibers at the bases of cut and broken fronds. We watched the bird store about eight acorns in 30 min. The storing behavior of this bird was identical to that of Acorn Woodpeckers (*M. formicivorus*) when the latter are not storing in prepared holes (MacRoberts and MacRoberts, Ornithol. Monogr. 21, 1976). A number of oak seedlings had sprouted in the "storage palms" indicating that acorns had been stored there in previous years.—M. H. MacRoberts and B. R. MacRoberts, *740 Columbia, Shreveport, Louisiana 71104.* *Accepted 31 May 1985.*

Wilson Bull., 97(4), 1985, pp. 571–572

Brown Noddy attacks mouse.—Predation upon live mammals is not common in terns (Sterninae), and the only dietary items reported previously for the Brown Noddy (*Anous stolidus*) are fish and marine invertebrates (Serventy et al., The Handbook of Australian Sea-Birds, A. H. and A. W. Reed, Sydney, Australia, 1971; Frith, The Complete Book of Australian Birds, Reader's Digest Services, Sydney, Australia, 1976; Brown, J. Anim. Ecol. 44:731–742, 1975; Ashmole and Ashmole, Peabody Mus. Nat. Hist. Bull. 24:1–131, 1967).

On 20 June 1981, during a vegetation survey of Long Island, a coral cay on Chesterfield

Reef, New Caledonia, I watched a Brown Noddy alight in a small patch of *Boerhavia* and seize a live mouse in its beak. The tern lunged forward several times, getting a better purchase on the mouse and apparently attempting to swallow it. The action took place about 4 m from me. When I approached closer and attempted to take a photograph, the mouse either escaped or was released by the bird, which then flew away. I attempted to catch the mouse, but it escaped into the vegetation. The only species of mouse known from the island is the introduced *Mus musculus*.

During mouse plagues, mice have been taken by Whiskered Terns (*Chlidonias hybridae*) and Gull-billed Terns (*Gelochelidon nilotica*) (Hobbs, Emu 76:219–220, 1976); the latter species also preys on lizards (Rohwer and Woolfenden, Wilson Bull. 80:330–331, 1968; Frith, 1976), as do Grey-backed Terns (*Sterna lunata*) (Clapp, Wilson Bull. 88:354, 1976). I am unaware of any records of species of *Sterna* feeding on mammals.

Brown Noddies nest mainly on coral cays, where small mammals are not usually found. Historically, noddies would have had little opportunity to take such prey. The present observation indicates that they have sufficient behavioral flexibility to take prey other than marine organisms on an opportunistic basis, and it represents the only known predatory attack by terns of this genus on a mammal.—Harold Heatwole, *Dept. Zoology, Univ. New England, Armidale, New South Wales, 2351, Australia.* *Accepted 30 Apr. 1985.*

Wilson Bull., 97(4), 1985, pp. 572–573

Eastern Screech-Owl captures goldfish in patio pond.—A search of the literature reveals that fish are included as an uncommon source of food for the Eastern Screech-Owl (*Otus asio*). Chapman (Handbook of Birds of Eastern North America, D. Appleton-Century Co., New York, New York 1937:337) reported that of 255 stomach contents examined (presumably by Fisher) only one contained fish. Rising and Schueler (Wilson Bull. 92:250–51, 1980) found vertebrae and other parts of a 5–6-cm fish in the stomach contents of a screech owl. Cope and Barber (Wilson Bull. 90:450, 1978) referred to Frazar as having found 16 horned pouts (Pisces: *Ictalurus nebulosus*) in a screech owl nest cavity. Other authors include, but not frequently, fish in the diet of screech owls. I have not found reference to an observation of screech owls capturing fish, and the one observation of this species in water was by Crowe (Wilson Bull. 65:207, 1953), who saw a screech owl bathing in a puddle of water 2.5–5.0 cm deep.

Adjacent to a wing of our home is a small, ornamental, semicircular fish pond, approximately 4.5–2.1 m wide and 0.7 m deep at the center. The pond is clearly visible from our living room through large sliding glass doors. Hanging ceramic pots of plants suspended from the overhanging roof are frequently used as perches by birds. After dark, the pond is brightly illuminated. On several evenings, an Eastern Screech-Owl had been seen clinging to a swaying pot and peering down toward the 15–25 goldfish (*Carassius auratus*) that feed at the surface. The depth of the pond is such that mammalian predators move slowly and inadequately through the water, enabling the fish to take refuge under overhanging rocks and in protected caverns. I have watched raccoons (*Procyon lotor*) move with difficulty through the deep water, unable to capture the goldfish; yet, the number of fish slowly declined without visible remains of the fish in the area. On 26 January 1984, well after dark (ca. 22:30), I observed a screech owl flying apparently out of the pond, for the disturbed water surface indicated that something other than fish had been in the water. Within 15 min I saw a screech owl drop directly down from an overhanging limb and enter the water feet first. Its head was held above the water and its widely outstretched wings were beating the

surface. Within 3–5 sec it took off with a goldfish, approximately 15 cm long, in its talons. It flew easily and swiftly in the direction of a nest box used each year by screech owls located high in a tree approximately 30 m distant at the far end of the patio. The next day I looked inside the box. There were no fish remains in the box or at the base of the tree. To my knowledge, this is the only observation of a screech owl descending into the water and capturing a living fish.—Kenneth W. Prescott, *Dept. Art, Univ. Texas, Austin, Texas 78712.* *Accepted 8 Feb. 1985.*

Wilson Bull., 97(4), 1985, pp. 574–590

ORNITHOLOGICAL LITERATURE

BIRDS OF NORTH AMERICA. Expanded, revised edition. By Chandler S. Robbins, Bertel Bruun, and Herbert S. Zim. Golden Press, New York, New York, 1983:360 pp., many colored paintings and range maps. $10.95 (hardbound), $7.95 (limpbound).—The "Robbins" guide hardly needs any introduction for the present-day birdwatcher. Since its first publication in 1966 it has earned a well-merited popularity with most birders. A revised edition, now at hand, is most welcome. It made its appearance three years after the revised edition of its major competitor and at a time when two new guides also became available.

Veteran users of the guide will find little change in the present edition. The new book is printed on a different grade of paper that results in greater clarity and more faithful reproduction of the figures. Most of the paintings have not been redone, but from the excellence of the reproduction I suspect that new plates were made from them. In some cases individual bird figures have been rearranged and some new species have been inserted into the old plates. There are 10 totally new plates that figure the exotic parrots now established in Florida and California, several of the Eurasian pipits that are almost regular along the West Coast, and a number of other Eurasian species that now occur in Alaska. I have not attempted to count the new species added in this edition, but I note that two—Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*) and Blue-gray Tanager (*Thraupis episcopus*)—have been eliminated. The former has not appeared in Arizona for many years, and indeed, may be extinct, while the introduced Florida population of the tanager has apparently died out.

The textual material has had only minor changes, a testimony to the accuracy of the earlier edition. A few corrections and additions have been made to the identification clues. Nomenclature follows the 6th edition of the A.O.U. Check-list (1983), but the arrangement of species in the book is essentially as it was in the older edition. However, the Table of Contents is arranged according to the 1983 classification.

A distinct improvement from the earlier edition is that the range maps are not only clearer and easier to read, but they are not all drawn on the same basic map. Species with limited distribution have somewhat larger maps. No political boundaries are shown on these maps, which makes for some difficulty in interpretation. All of the maps have been redrawn to represent current knowledge of the ranges.

Vocalizations are again mostly illustrated by sonagrams, which are helpful to some people but not to others. The description of the songs in the text are usually not very useful.

In the review copy, the color reproduction seems to be better than in my copies of the original edition, and only two plates seem to be out of register. The only fault I find with the color is that the shade of green used gives the wrong impression of the true colors of the *Empidonax* flycatchers and the fall warblers. In fact, I do not care for Arthur Singer's plates of the fall warblers at all. Not many people unfamiliar with the species could identify the fall Blackpoll from his figure. Of the guides currently available the National Geographic Society Guide has the best, albeit flawed, portraits of the fall warblers. Is there a market for a specialized guide for the fall warblers, and if so, are there an author and an artist willing to do it?

In summary, this edition continues the fine precedent set by the original, and those people who have "grown up" using "Robbins," as well as newcomers to the birding fraternity, will enjoy the book and will profit from its use.—GEORGE A. HALL.

FIELD GUIDE TO THE BIRDS OF NORTH AMERICA. By Shirley L. Scott (ed.). National Geographic Society, Washington, D.C., 1983:464 pp., many color plates. $15.95.

GUIDE TO BIRD SOUNDS. Produced by James L. Gulledge. National Geographic Society, Washington, D.C., 1983. Four 9 in. 33.3 records. (No price given.)

THE WONDER OF BIRDS. By Robert M. Poole (ed.). National Geographic Society, Washington, D.C., 1983:280 pp., many color photos. (No price given.) $29.95 for the package of three items plus a poster-sized migration map. (Obtainable only from The Society.)

We are currently suffering from a plentitude of good field guides. The two old-timers in this area each have had new editions recently (see review in the Bulletin, 93:425–427, 1981, and above; and more recently a three-volume "advanced" guide has appeared (reviewed in the Bulletin, 96:322–326, 1984). Now we have before us, as a part of a general package on birds, a new field guide from the venerable National Geographic Society. This review will dwell mostly on that guide which, despite the difficulty of obtaining it, is likely to be of great interest to most birders.

The guide is sturdily bound with a paper cover, and should be capable of standing up under heavy use. It is, however, too large to fit into most pockets; but my observations of many birders equipped with an assortment of pouches and carrying cases would make this seem to be of no great disadvantage. The scope of the guide is all of North America, as defined prior to the 1983 A.O.U. Check-list. The format consists of a colored drawing (sometimes several) of each species on the page opposite the textual material that includes a small distribution map. A total of 13 artists made the drawings, and for once it is easily possible to allocate a given portrait to the proper artist. The text was apparently compiled by a committee and it is never possible to pin down the attribution of any particular statement. Four persons are listed as "consultants" for this book, including two well-known ornithologists and two well-known experts on field identification.

The book opens with the usual preliminary matter, including the obligatory figures defining the names of bird parts and comments for beginners in the study of birds. The species accounts then follow in approximately the order of the 1983 A.O.U. Check-list, and the nomenclature of that list is followed. The index serves also as a place for the birder to check off his "Life List."

Let us examine the poorest aspect of the book first—the range maps. The summer and winter ranges are plotted on small maps measuring 2.5 × 2.1 cm. There is no indication of migration routes, which, in many cases, leads to confusion. For example, the Pectoral Sandpiper (*Calidris melanotos*) is shown as breeding on the shores of Hudson Bay, and on the Arctic Ocean in the Northwest. No winter range is shown, and the novice (or even a more experienced) birder has no way of knowing that this species may occur almost any place in the United States during migration. He might assume that this species was as localized as is the Buff-breasted Sandpiper (*Tryngites subruficollis*) which has a similar breeding range given on the same page. The small size of the maps, showing most of North America, leads to considerable exaggeration of the ranges of those species that extend south along the highlands of the Appalachians, the Rockies, or the Sierra Nevada. Thus some species found only on the highest mountains of the Appalachians are represented as occurring throughout the small state of West Virginia. Elsewhere the ranges are a little less misleading, but the maps are of minimal utility. For a few highly localized species, as for example Florida specialties, larger scale and more informative maps are used.

The descriptions of vocalizations leave much to be desired. While some use the standard phonetic syllabifications, others are less informative. Thus the song of the Canada Warbler (*Wilsonia canadensis*) is said to begin with one or more short chips that continues as a rich and highly variable warble. In copies of the guide that are part of the three-item package,

species that can be heard on the records of "Guide to Bird Sounds" are so indicated, but this indication is omitted from copies of the guide sold alone. Those species that are on the recordings have the poorest textual descriptions, a disservice to those who buy only the "Field Guide."

Finally, let us consider the pictures and the accompanying text as identification guides. More plumages are illustrated in this guide than in most. For many groups, such as the shorebirds, a clear distinction is made between the fall plumage of adults and that of first year birds, something that has been badly confused in earlier guides. The gulls are very well illustrated, as for example six different plumages being shown for the Herring Gull (*Larus argentatus*). There are also flight pictures of waterfowl, shorebirds, and raptors (oddly of only the female hawks). I would judge that the latter would not be as useful for identification as are the more stylized drawings in the original Peterson guides. A special feature is the large number of Eurasian species figured on the basis of occasional records in Alaska. As the inevitable consequence of bringing these species to the attention of bird watchers, I predict a rash of "sight records" of these species in the eastern United States.

In general, the reproduction of the paintings is excellent, and none seems to be out of register. Some species, which in the field usually appear to be all black, show too much color, such as a "blue" California Condor (*Gymnogyps californianus*) and "green" cormorants. The yellow on some of the flycatchers is too bright. To my eye, a great many of the pictures are displeasing. All the pertinent field marks are correctly given in most cases, and the birds can be identified, but somehow, most of the small passerines appear to be misshapen. Most of the artists seem to have trouble correctly drawing the face and "chin" of a small bird. The *Catharus* thrushes are shown in a peculiar "hunchbacked," neckless posture; the swallows and swifts (shown flying) are quite misshapen, and the Black-and-White Warbler (*Mniotilta varia*) is simply grotesque. There was no attempt to draw all the species on a given plate to the same scale, and so the beginner may become confused by such things as an American Woodcock (*Scolopax minor*) half again as large as a Common Snipe (*Gallinago gallinago*). There are, in fact, a good number of outright errors in detail but space here prevents a detailed listing of them.

As in the case of all field guides now available, some of the fall warblers are very poorly done: Blackpoll (*Dendroica striata*) (the same old confusion about the color of the legs), Bay-breasted (*D. castanea*), western Palm (*D. palmarum*) (these are often quite yellow), and Tennessee (*Vermivora peregrina*) (poorly done in all plumages). But, overall, the treatment here is the best yet. Fall warblers are not "confusing" to many people, and we can hope that someday a guide will make use of this expertise.

I would rate the text as superior to the portraits in most cases. Frequently I found something in a figure that was not quite correct, only to note that the text had things right.

Despite my negative remarks given here, I do feel that this guide rates very highly in comparison with its competition. It is the first field guide to recognize great variability in many species. With careful study of both text and figures, a birder should be able to identify any species unfamiliar to him. He will have trouble identifying songs and he may get fooled on distribution, but on balance he will find the guide helpful and useful.

The "Guide to Birds Sounds" consists of four "floppy" records containing noises (not all are vocalizations) of 179 species. The recordings are from the Cornell Library of Natural Sounds and are very well done. I can see no obvious rationale behind the selection of species. There are songs of only six wood warblers (including the possibly extinct Bachman's [*V. bachmanii*]) and none for the common eastern sparrows. Eighty-two of the species are nonpasserines, including 20 shorebirds, but no ducks and only three hawks are represented. One of the shorebirds is the accidental Temminck's Stint (*Calidris temminckii*). The selection

of species, however, is nicely balanced between eastern and western species. One wonders about the permanence of these flimsy plastic records.

"The Wonder of Birds" is an attractive "coffee-table" book suitable as an introduction to birds for the beginner. There are seven chapters written by Louis J. Halle, Roger F. Pasquier, Paul A. Johnsgard, Anne LaBastille, Frank Graham, Jr., Franklin Russell, and George Laycock. These cover such topics as the migration seasons, the breeding season, the diversity of birds, and two chapters oriented towards conservation. This material is well written and should be informative to the tyro. The style is several cuts above the usual National Geographic style. Even experienced birders and ornithologists, however, will find much of interest in this magnificent collection of color photographs.—George A. Hall.

The Birds of the Republic of Panama. By Alexander Wetmore, Roger Pasquier, and Storrs L. Olson. Passeriformes: Hirundinidae (Swallows) to Fringillidae (Finches). Smithson. Misc. Collect. Vol. 150, Part 4, Smithsonian Press, Washington, D.C., 1984:670 pp., 1 color plate. 49 figs., 16 × 23 cm. $29.95.—Alexander Wetmore died in 1978 having finished but a small part of this last volume of his major work. He began field work for these volumes in 1946, and the first volume, covering up to the gulls, was published in 1965 (now $25.00). The second volume, pigeons to woodpeckers, was published in 1968 (now $25.00), and the third volume, published in 1972, entered the passerines up to the Oxyruncidae (sharpbills) (now $25.00).

With the encouragement of S. D. Ripley, Roger Pasquier took on the job of writing the rest of the species accounts. Storrs Olson became responsible for the systematics portion, which included the analysis of several thousand specimens. By using "I" for Wetmore and his own literary skill, Pasquier has very successfully mimicked Wetmore's gentle and scholarly style. This fourth volume, like the others, centers on the taxonomy and distribution of species whose ranges often greatly exceed the political boundaries of Panama. The families follow the Wetmore sequence, an arrangement also followed by R. Ridgely's "A Field Guide to the Birds of Panama" (Princeton Univ. Press, 1981). Pasquier and Olson sensibly follow this and not the system of the A.O.U. Check-list of North American Birds (6th edition, 1983), which extended its coverage to the Panamanian-Colombian border.

Each family is briefly described and, for those with several species in Panama, a traditional key follows. This is by no means a jet-setter's field guide; but for identifying difficult species in the hand, as from a mistnet, it is often superior to the color plates and broad descriptions of the guides. The black-and-white drawings by Guy Tudor and the late Walter Weber are often attractive and thus appropriate, but they offer little aid in identification. The color frontispiece is of *Dacnis viguieri,* a little known endemic coerebid from the Panamanian-Colombian border. The reproduction in my copy is too yellow.

Each species account covers the scientific, English, and Spanish names, citing the literature on the nomenclature, taxonomy, distribution, breeding status, and aspects of the natural history both within and outside of Panama. For polytypic species like the Yellow Warbler (*Dendroica petechia*) with seven races recorded from Panama, the authors follow Wetmore's apparently "old-fashioned" style of discussing each subspecies separately and at the same level of the nominate form. Sounds dull, but it isn't. I was fascinated by the differences that the keen-eyed Wetmore found not just in the color and size of museum specimens but also in behavior, voice, and habitat selection among the various races. Such information is almost unique and is fodder for students of avian evolution. Pasquier and Olson, following Wetmore's wide knowledge of the literature, have included references and discussion of the findings of other workers ranging from the latest DNA taxonomic interpretations to the fat

condition and possible flight range of migrants about to visit the Temperate Zone. With the appearance of Ridgely's guide in 1981, a torrent of new records and range extensions has occurred. Much of this information went to Eugene Eisenmann, who was always in close correspondence with Wetmore, and to Ridgely. Practically all of this information has found its way into Volume 4. The authors have included a 15-page appendix of the species (beginning with penguins) recorded or collected since the publication of the previous volumes.

In the first volume Wetmore declared his intent to include a bibliography of the avifauna, an overview of all the species, and a gazetteer. This has not, and possibly never will, come about. Pasquier and Olson forthrightly point out that to have attempted those goals might have resulted in no publication whatsoever. I am sympathetic with this view, but the lack of even a simple map showing the locations of the major localities and provinces is most unfortunate. One needs only to open the cover of Ridgely (1981) to alleviate partly this omission.

There are relatively few significant typographical errors. The Spanish names are mainly translations of sometimes awkward English names and mean nothing to the local people of Panama. The classical North Temperate ornithological anachronism of "wintering" in the tropics is unfortunately retained throughout. Most such migrants live most of their lives under selective pressure peculiar to the tropics where winter does not occur. Why some exploit the annual protein bloom of the Temperate Zones and others do not is, of course, an interesting topic. The authors have not ignored the natural history of migrants in Panama.

The total cost of each volume purchased separately is $104.95; however, the Smithsonian Press offers the four volumes together for $85.00. For the wealth of information contained, that is a bargain. I am learning much from reading it.—Neal G. Smith.

Seabirds of Eastern North Pacific and Arctic Waters. By Delphine Haley (ed.), Pacific Search Press, Seattle, Washington, 1984:214 pp., 90 color photographs, 101 maps, numerous drawings. $39.95.—In this book the editor and authors have attempted to produce a work combining the esthetic qualities and readability of a "coffee-table book" and the usefulness of an up-to-date review of the biology of northeastern Pacific seabirds. With certain qualifying remarks, I feel that they have fulfilled their objectives.

The format is straightforward. An introduction by the editor covers oceanography as it relates to seabirds and an overview of the classification of seabird orders and families. The interaction of seabird populations and humans, from native cultures to modern commercial fishing and pollution, is also discussed. Ms. Haley has a pleasant, easily understood writing style that is filled with evocative descriptions of the wonderful and varied lifestyles of marine birds. Although mostly accurate, her text includes outrageous generalizations such as, "Few seabirds can afford to care for their young for very long." Confusing statements such as, "Nor can the sexes be distinguished by their behaviour, unless the actions are specifically attributable to male or female" also are not helpful. In the "Making of a seabird" chapter, the young of Kittlitz's (*Brachyramphus brevirostris*) and Xantus' (*Synthliboramphus hypoleucus*) murrelets are stated to be precocial: "(the young) only two to four days after hatching, flutter and fall to the sea." In reality only the latter's young are precocial. Kittlitz's Murrelet young are semiprecocial and remain at the nest site for many days before departing to sea. Another muddling of the facts concerns the lobed toes of phalaropes (*Phalaropus* spp.), which are stated to have evolved through the reduction of webbing, "an adaptation which presumably makes it easy for the birds to twirl about rapidly."

Fortunately, the chapters on each seabird family, prepared by selected authorities, are well written and factually accurate. I found the chapters on the Procellariidae and Phae-

thontidae to be among the most interesting and informative in the book. The authors of these and the other chapters share with us their knowledge of and enthusiasm for their study species. The use of only English measures (weights are given in pounds and ounces throughout the text) may be annoying to those who use metric measures, now standard in scientific literature. In the section on the Alcidae the author states that there are about 5.7 million Common Murres (*Uria aalge*) in North America. Totals for each West Coast state and province add up to approximately this figure. No explanation is given for the omission of the 1.3 million Common Murres breeding in eastern Canada.

The range maps are the most disappointing aspect of this book. Aside from suffering from lack of detail and clarity due to the small scale and poor methods of indicating range (crude hatching and bloblike stars), most illustrated ranges have errors, and many are grossly inaccurate. A few of the more conspicuous examples of this problem deserve mention. The sea ranges of Townsend's (*Puffinus auricularis*) and Wedge-tailed (*P. pacificus*) shearwaters are shown to include coastal southern and central California, where they would occur only as accidentals. The sea ranges of Wilson's Storm-Petrels (*Oceanites oceanicus*) and Magnificent Frigatebirds (*Fregata magnificens*) are similarly dubious. The range maps of the alcids are particularly poor. Major breeding areas of Ancient Murrelets (*Synthliboramphus antiquus*) are shown to include the mainland coast of British Columbia, Vancouver Island, and northern Washington. In reality, this species breeds nowhere south or east of the Queen Charlotte Islands. Queen Charlotte Strait in British Columbia is indicated as a major breeding area for Horned Puffins (*Fratercula corniculata*), when, in fact, their southernmost colony is at Forrester Island, Alaska, 800 km to the north. Even allowing for the fact that the ranges of many seabirds are inadequately known, the inaccuracies of these maps are inexcusable as they ignore information on distribution readily available in the literature. The maps, contrary to what is said on the back cover of the book, do not set a new standard.

The photographs appear to have been chosen carefully and are generally excellent and appropriate to the accompanying text. Two have inaccurate captions. An adult winter-plumaged Thayer's Gull (*Larus thayeri*) is the most conspicuous gull in a photograph labeled as showing Herring Gulls (*L. argentatus*) and Northern Fulmars (*Fulmarus glacialis*). A photograph of a Red Phalarope (*Phalaropus fulicaria*), indicated as being a bird in winter plumage, appears to be a juvenile.

A number of excellent drawings, which complement sections of text, are included. With one exception, these illustrations are flawless. A drawing, intended to be of a phalarope inspecting parasitic crustacea on a whale's back, pictures some other type of shorebird (*Calidris* or perhaps *Heteroscelus*?).

Despite some rather conspicuous errors, a number of minor flaws, and the unfortunate quality of the range maps, this is an esthetically pleasing and very informative book. Seabird lovers, birders, and naturalists would do well to consider purchasing this book.—Ian L. Jones.

The Birds of Indiana. By Russell E. Mumford and Charles E. Keller, illus. by William Zimmerman. Indiana Univ. Press, Bloomington, Indiana, 1984:376 pp., 183 color plates, 2 state maps, 1 chart. $75.00.—This very handsome book presents information on habitat, seasonal occurrence, breeding biology, and Indiana distribution of 170 species of birds breeding within the state. Useful data on clutch size, characteristic vocalizations, food, unusual concentrations, and historical occurrence in Indiana are given. There are also species accounts for nonbreeding birds, but they are not illustrated, and the text is in smaller print than for the breeding species. The two maps show the counties and physiographic regions of Indiana. Unfortunately, state distribution maps for each species are not presented.

The illustrations of the breeding birds, their nests, and eggs are very pleasing, and some of the bird portraits are exceptional works of art. Those of the nests, however, are often poorly characterized. The settings for nests showcase state flowers, and the effect is lovely, although somewhat dubious ecologically. For example, it seems unlikely that the early spring flowers of the wild plum (*Prunus* sp.) would still be present when Orchard Orioles (*Icterus spurius*) nest. One wonders at garden phlox (*Phlox* sp.) towering above the nest of a Yellow-billed Cuckoo (*Coccyzus americanus*), whose nest is usually placed at heights much above that of this flower. And what a rare coincidence it must be to find the nest of a Yellow-crowned Night-Heron (*Nycticorax violaceus*) in an umbrella magnolia (*Magnolia tripetala*), or that of a Scarlet Tanager (*Piranga olivacea*) in a yellowwood (*Cladrastis lutea*).

There are a few typographical errors (e.g., p. 182, "next" for "nest"). On p. 191, the statement is made that only the nest of the Least Flycatcher (*Empidonax minimus*) is shown, when actually nests of three species are depicted. On p. 226, the text states that a nest contained three eggs "and two naked pairs of birds," obviously an error. In the introduction (p. xviii), the authors claim that Indiana has more breeding species than Illinois or Kentucky. This was not true in 1963 (according to R. T. Peterson in "The Birds," Life Natural History, Time, New York, New York), nor is it true for Illinois at present. The boldface type in the Index scarcely distinguishes the page numbers of illustrations. These minor flaws do not really detract from the book.

In general, the style of writing is anecdotal and more interesting to read than a listing of data would be. On the other hand, the birders of Indiana have published reams of good data on birds in the state. If the authors had presented this information in some comprehensive form, "The Birds of Indiana" would have been a great book (though it might have taken years to write). For example, Keller's (1957–1958) papers in The Indiana Audubon Quarterly present much additional quantitative data on shorebirds. Lastly, the book is often unclear about the source of material; one assumes that much of it was previously unpublished, but it would be nice to know if this is true.

Though intended for a wide audience, this plush book is too expensive for students and too general to serve as a technical reference. It is attractive and should appeal to affluent bird watchers and to those who enjoy bird art.—Jean W. Graber.

Species of Special Concern in Pennsylvania. By Hugh H. Genoways and Fred J. Brenner (eds.). Carnegie Museum of Natural History, Special Publication Number 11, Pittsburgh, Pennsylvania 1985:vi + 429 pp., 6 color plates, black-and-white photos of over 100 species, 350 maps. $30.00 plus $3.00 shipping and handling.—This is the latest, and certainly the most sumptuous, statewide listing of species of special concern. Individual species are classified as: Endangered, Threatened, Vulnerable, Status Undetermined, Extirpated, and Recently Extinct. The format of these accounts seems constant for all the states so far represented, with sections on Description (very brief), Range, Habitat, Life History and Ecology, Basis for Classification, Recommendations, and Selected References. For each species a map of the continental range and a Pennsylvania map showing specific records, usually only by county, is given.

There are informative introductory chapters on Aquatic and Terrestrial Habitats, Physiographic Provinces, Drainage Patterns, and Definitions of Species Categories. These are followed by chapters covering 21 endangered plants, 62 invertebrates (mostly Lepidoptera and Odonata), 62 fishes, 18 reptiles and amphibians, 39 birds, and 34 mammals. The individual accounts are written by many people, and each chapter is prepared by a specialist editor.

The chapter on birds is edited by Frank B. Gill, and the accounts were prepared by Frank

Haas, Barbara Haas, and John A. Ginaven. The species included as Endangered are the Bald Eagle (*Haliaeetus leucocephalus*), King Rail (*Rallus elegans*), Short-eared Owl (*Asio flammeus*), and Bewick's Wren (*Thryomanes bewickii*). The Least Bittern, (*Ixobrychus exilis*), American Bittern (*Botaurus lentiginosus*), Upland Sandpiper (*Bartramia longicauda*), Black Tern (*Chlidonias niger*), Sedge Wren (*Cistothorus platensis*), and Henslow's Sparrow (*Ammodramus henslowii*) are considered Threatened. The Extirpated list includes Osprey (*Pandion haliaetus*), Peregrine Falcon (*Falco peregrinus*), Greater Prairie Chicken (*Tympanuchus cupido*), Piping Plover (*Charadrius melodus*), Common Tern (*Sterna hirundo*), Loggerhead Shrike (*Lanius ludovicianus*), Dickcissel (*Spiza americana*), Bachman's Sparrow (*Aimophila aestivalis*), and Lark Sparrow (*Chondestes grammacus*); and the Passenger Pigeon (*Ectopistes migratorius*) is Extinct. Twelve species are considered as Vulnerable and seven as Status Undetermined. One might quarrel with the inclusion of some of these species, but the recommendations of a large group of bird students were available to the writers.

In many cases the species accounts honestly admit that real knowledge of the species is lacking, and most of the recommendations advocate additional research. Despite this limitation, this is a valuable compilation of current knowledge.

In some cases the picture is quite gloomy, but in others puzzling and challenging elements of mystery enter. Why, for example, should the Henslow's Sparrow suddenly have changed from a widespread, and often common nesting bird, to a threatened species? This has occurred in other states besides Pennsylvania. Although Pennsylvania was always on the edge of the breeding range of Bachman's Sparrow, the species has disappeared from other places, such as central West Virginia, where it was common 40–50 years ago. Such mysteries abound, but we can only guess as to the answers.

While the material in this book is valuable from a historical aspect, much of it will be obsolete in a few years. The status of many species will no doubt change rapidly, and much new information will come to light. One can wonder at the wisdom of publishing the book in such a handsome and expensive way.—GEORGE A. HALL.

THE BIRDS OF SAN DIEGO COUNTY. By Philip Unitt. Illustrated by Allan Brooks. Memoir 13, San Diego Society of Natural History, 1984:xxiii–276 pp., 12 habitat photos, 129 maps, 12 colored plates. $20.00 ($14.00 paperbound; $500.00 patrons' edition) plus $2.00 postage and handling in U.S. (foreign extra); California residents add 6% sales tax. (Order from San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112.)—This large, handsome book, with 12 previously unpublished paintings by the famous Allan Brooks, updates the avifauna of a well-known yet poorly understood microcosm.

Why, of all our thousands of counties, does San Diego alone seem to warrant regular reviews of its avifauna (1919, 1959, 1984, besides the reviews of southwestern California in 1912 and 1933)? Partly this is because San Diego County is more diverse and complex, ecologically and faunally, than most states or provinces. Though islands lie just outside its borders, it still ranges from open ocean, rocky and foggy seacoast, and salt marsh, up through diverse plant associations, to cool pine-oak forests (with firs), from which it drops through junipers and scrub to arid, sun-baked desert whose arroyos and mountains have their own special associations. A well-illustrated chapter discusses geography and vegetation. Several associations, and their attendant birds, are already decimated. These include marsh, coastal sage scrub, and the vital riparian strands; the original fauna of the native coastal grasslands will never be known. Biocides, parasitic cowbirds, "development," and other threats contribute to declining bird numbers. As Unitt observes, "Short-term planning by government agencies is the most serious enemy that the Least Tern [among others?] faces in the long run."

Against this, as elsewhere, additional species, subspecies, and rarities arrive, or even breed in new or overlooked localities (as detailed for 1982 and 1983 in an appendix). Few regions, of course, are immune to human degradation today (islands are usually in the worst condition); and some other California counties are also diverse and complex. So why is San Diego so special?

The preeminence of San Diego County stems from the tradition of perceptive, detailed analysis, and publication maintained by the San Diego Society of Natural History and its capable co-workers. Interest seldom ends at the species or "resident" level. The quite different status and breeding seasons of species like Costa's Hummingbird (*Calypte costae*) and *Phainopepla nitens* in different parts of the county are duly detailed. Fox Sparrows (*Passerella iliaca*) are now present all year, but collecting and careful study show that the county is a winter meeting place for Fox Sparrows from much of the continent to the north. Though Unitt tentatively synonymizes six A.O.U. races of *P. iliaca,* he still credits the county with seven races—all collected except *stephensi,* the one now presumably breeding. Despite the supposed adequacy of present museum collections—loudly proclaimed by those with no idea of their importance and uses—the main wintering grounds of this distinctive swollen-billed race remain unknown in 1985!

Pipits (*Anthus* spp.) converge on San Diego County from even beyond North America. Yet the continent-wide Common Nighthawk (*Chordeiles minor*) is at best casual, with no known county specimen. Among other points shown by subspecies is that the only lowland specimen of Pygmy Nuthatch (*Sitta pygmaea*) is also a migrant, not an altitudinal wanderer.

Subspecies groups are discussed separately in some cases, such as "Black-tailed" Gnatcatchers (*Polioptila* "*melanura*"). (The *lucida* race shows vocal differences and possible sympatry with *californica,* which has seriously decreased.) Unitt makes original contributions (often based on limited material) to our knowledge of the distribution or characteristics of some subspecies (*Nycticorax violaceus, Empidonax difficilis, E. traillii, Progne subis, Hirundo pyrrhonota*). In extending the range of *E. traillii extimus* (ignored by A.O.U., but see Wetmore, Part 3:478, 1972), Unitt also raises another conservation problem for California: we can preserve biological diversity only through *knowledge* (study and judgment), not through ignorant, sentimental protection of menaces (gulls, starlings, cowbirds) or willful, prejudiced biopolitics.

Unitt's manuscript evidently antedated the 1983 A.O.U. Check-list. Still, his "Emberizidae" agrees with the check-list at the subfamily level—avoiding, however, some of the A.O.U.'s inexplicable anomalies, such as inserting *Sturnella* between *Agelaius* and *Xanthocephalus,* and various unrelated genera between *Aimophila* and *Amphispiza* (which Unitt unites). Otherwise he essentially follows the classic Wetmore–A.O.U. 1931–1957 classification. Procellariiformes precede loons (*Gavia*) and Podicipedidae; Anseriformes follow Falconiformes, bringing Cathartidae next to the related Ciconiiformes; Laniidae and vireos follow Corvidae; Carduelinae precede Emberizidae; Recurvirostridae precede both Charadriidae and Scolopacidae (with no other less-related groups separating them as in the 1983 A.O.U. Check-list); Bombycillidae include A.O.U.'s Ptilogonatidae; etc. In part, this follows anatomical researches by Rea ("Once A River," Univ. Arizona Press, Tucson, 1983). By "this unorthodox approach," including departures from A.O.U. names, Unitt hopes to spark "increased interest in the wondrous complexities of bird evolution." Fortunately these books are well indexed, with tables of contents—a necessity since the uncalled-for "Basel Committee" (which was supposed to "end confusion") unleashed the rash of inexplicable departures from the classic Gadow-Ridgway-Wetmore sequence. (Among Unitt's minor inconsistencies, the species list, pp. 245–258, occasionally disagrees with the text in order or nomenclature; cf. *Mergus* spp., *Catoptrophorus,* "*Tringa hypoleucos*".)

The weakest point, scientifically, is Unitt's apparently excessive reliance on sight reports

in "Audubon Field Notes" and "American Birds." In most places this would be ruinous. In southern California it is much less so because of the critical attitude, influence, and editing of Guy McCaskie. Still, no one can identify, with scientific certainty, photographs in critical genera—much less birds not photographed or collected before they flew out to die at sea. The most perfect of photographs simply cannot give us measurements, etc., nor evidence of tell-tale feather damage or lengthened claws of escaped individuals. Unitt recognizes this uncertainty at times (*Calidris ruficollis*), yet includes the species in his list of 445 native species (plus at least 89 subspecies) recorded. More careful researchers elsewhere have shown that well-known species "recorded" widely and regularly, or even abundantly in winter, are not actually present (Devillers, Auk 94:417–429, 1977, [*Catharacta skua*]; Phillips, Am. Birds 29:799–806, 1975 [*Calidris pusilla*]). Though Unitt is usually careful to specify important specimen records in his text, one must turn to the list of species to find that *Dendroica caerulescens* has been taken but *D. dominica* has not.

Still, Unitt lists two races of *D. dominica*, as well as *Vermivora celata celata* (one dubious specimen, not reexamined, plus sight reports). Deficient collecting is obvious again and again, not only in warblers but in many critical groups—even the notorious *Empidonax* flycatchers, *Catharus* thrushes, the endlessly variable *Eremophila* larks, and the Song Sparrow (*Melospiza melodia*) on which one might expect ornithologists to have concentrated. No one in San Diego cares to skin one of the still-common *Cathartes* vultures, nor are skeletons with measurements cited; yet vultures are often found dead. Even dead accidentals are often not preserved in any form (two of the three *Cyclorrhynchus* auklets, both *Bombycilla garrulus* waxwings); nor is the migrant Flammulated Owl (*Otus flammeolus*), which was caught on a ship and used in an experiment, now to be found. Occasionally, critical specimens are still mounted (one of the two *Regulus satrapa* kinglets). No matter how customary this lack of specimen collection is or was, it is *not* good, permanent science, and our successors will not be grateful.

The subspecies discussions would occasionally be more meaningful if the localities represented were specified (e.g., *Auriparus flaviceps*). Perhaps in the future, bar graphs of seasonal occurrence will help visualize migrations of some distinctive subspecies, or at least of species. We have much to learn, as Unitt points out in the case of the occasional summering Summer Tanagers (*Piranga rubra* subsp.?). Yet so much has been accomplished in this border county that one is again (or still) impressed by how neatly concentrations of migrants and "ranges" of rare winter visitors "end" exactly at the Mexican border!

Though the major eastern museums were not consulted, Unitt still gives many historic data. Terms (common, rare, etc.) are numerically defined (p. 3). He gives many counts and egg dates. The 126 maps of breeding distributions (of 129 species) carefully distinguish present and former, definite and probable, and published and unpublished breeding locations.

This first expanded summary is an original, worthwhile, up-to-date digest of a vast amount of data. In many ways it can serve as a model for other regional reports. San Diego County and its museum are to be congratulated. But there is still much to do even here—both in specimen collection and in habitat protection.—Allan R. Phillips.

Perspectives in Ornithology. Essays Presented for the Centennial of the American Ornithologists' Union. By A. H. Brush and G. A. Clark, Jr. (eds.). Cambridge University Press, New York, New York, 1983:x + 560 pp., 36 text figs., 11 tables. $29.95.—This book, devoted to reviewing important "frontier" areas of ornithological interest and research, consists of 13 chapters and an Introduction by Professor Ernst Mayr. Dr. Mayr sets the stage by documenting the leading role that ornithology has played in the development of

modern biological thought. Ornithology, evolutionary biology, and biogeography have been associated closely for a hundred years. Much of our knowledge of geographic speciation was developed from birds. Pioneer studies in animal behavior were carried out on birds, and birds remain a core group for work in this area. Modern knowledge of biogeography, geographic variation, animal navigation, and community ecology stems largely from avian studies. Dr. Mayr's introduction makes one feel proud to be an ornithologist.

The first two chapters are general in nature. They deal, respectively, with the conservation of rare birds in captivity (William Conway) and the role of museum collections (Jon C. Barlow and Nancy J. Flood). Four chapters are devoted to aspects of behavior: "Avian mating systems" (Douglas W. Mock); "Cooperative breeding strategies among birds" (Stephen T. Emlen and Sandra L. Vehrencamp); "Bird song learning, theme and variations" (P. J. B. Slater); and "Bird navigation" (Charles Walcott and Anthony J. Lednor). Two major areas of contemporary ecological research are reviewed: "Ecological energetics: what are the questions" (Glenn E. Walsberg) and "Perspectives in optimal foraging" (John R. Krebs, David W. Stephens, and William J. Sutherland). A noteworthy new review of Mesozoic and early Tertiary avian fossils is provided by Larry D. Martin ("The origin and early radiation of birds"). Current thinking and controversies in avian community ecology and biogeography are reviewed by John A. Wiens ("Avian community ecology: an iconoclastic view") and Daniel Simberloff ("Biogeography: the unification and maturation of a science"), respectively.

All of the chapters are comprehensive. Additional breadth is given by the addition of discussants, who commonly were chosen because their views contrasted with those of the major contributor. The chapters are supported by extensive bibliographies. Wiens' chapter has a magnificent 207 titles; Simberloff's has 199.

It is impossible to comment on the highlights of individual chapters and the wealth of material contained therein. Most chapters are structured to include a brief history of the subject, provide a summary of major theories and concepts, and then treat current data in detail. Often a final statement suggests where the author thinks the subject is going; this is helpful. The reader thus comes away with a nicely balanced account. This reviewer found the chapters of Wiens and Simberloff highly rewarding. In both, complex and controversial subject matter is explored thoroughly, and a balanced overview is presented.

This book is a credit to the American Ornithologists' Union. It will be a basic reference for years to come.—Allen Keast.

The Heron Handbook. By James Hancock and James Kushlan. Harper and Row, New York, New York, 1984:188 pp., 66 color plates, 18 line drawings, 61 maps. $24.95.—Recently, considerable research has been conducted on the members of the Ardeidae. This book on herons and bitterns is an authoritative survey of current knowledge about the worldwide family of wading birds, incorporating recent research on the behavior and ecology of the group. The plumages, feeding and breeding behavior, and ecology of each of the recognized 60 species are discussed, and every species is illustrated with paintings by Robert Gillmor and Peter Hayman. Particularly useful are the four color plates illustrating every color phase of every race of the white herons and egrets. The small size of the book (9 × 6 in.) makes it easy to carry on travels abroad, although it is not field guide size.

The book is based on "The Herons of the World" by James Hancock and Hugh Elliott, first published in 1978. It has been updated and revised, includes new range maps for all species, and contains all the original plates plus the four new identification plates. From my perspective the organization and design are far superior to the original. It contains more up-to-date information and is smaller and easier to read. The new version contains much more information useful to scientists, yet is no less enjoyable reading.

The book begins with introductory chapters on classification, courtship, feeding, and identification of herons and egrets. These sections are brief, but provide an excellent overview of the topics with adequate references. The section on courtship even describes displays, giving the display names in boldface for easy location. The feeding section is superior, giving an overview of postures and movements, as well as a discussion of feeding strategies. Many of the examples therein are the North American herons that Kushlan has worked with. The line drawings in this and other sections clarify the displays.

The remainder of the book consists of species descriptions, including nomenclature, identification, distribution and population, habitat, migration behavior, and nest, eggs, and young. Each account gives a general overview of what is known about the species. The migration sections are usually brief, indicating our lack of knowledge about this subject. Habitat information is general, and I would have liked to see an overview table showing diversity of both feeding and nesting habitat preferences for all herons (or groups of herons).

The book would be more useful if the sections on breeding were expanded to provide more details and references for the serious student. The species accounts are informative and, in some cases, thought-provoking. They are necessarily brief, but adequate references are given to further research results on specific topics. The brevity of some of the accounts indicates where future contributions can be made.

I would have liked to see a concluding chapter comparing the behavior and ecology of the heron species. The authors clearly can provide a synthesis of the comparative behavioral adaptations of herons, including evolutionary implications; perhaps this is outside the scope of the volume.

I found the book to be an improvement over the original version not only because it has been updated, but because of the additional information on foraging and other behavior. The color plates are of better quality than the original, and the size makes it easier to carry, store, and use. The line drawings and range maps are particularly helpful, and make the book more attractive. Overall, I believe the volume is essential for any serious student of herons and for anyone traveling to parts of the world where they are unfamiliar with the resident species. It will be extremely valuable for graduate students interested in working with herons, and to nonspecialists wanting an overview of herons in general and of individual species in particular. I recommend it highly.—JOANNA BURGER.

THE CATTLE EGRET: A TEXAS FOCUS AND WORLD VIEW. By Raymond Clark Telfair II. Texas Agricultural Experiment Station, Texas A&M University, College Station, Texas, 1983:114 pp., many tables, figures, and maps. $16.95 (cloth), $10.95 (paper).—As a result of its spectacular range expansion in the New World, the Cattle Egret (*Bubulcus ibis*) has been the subject of much study. Telfair's monograph attempts to provide a comprehensive review of this research, while at the same time emphasizing work done on the species in Texas. All aspects of Cattle Egret biology are covered, beginning with an introduction that discusses the taxonomic status and world-wide range expansion of the species. Chapter 2 provides an historical perspective of changes in the range of the species within Texas. Chapter 3 discusses seasonal distribution and migration, while Chapters 4–7 deal with nesting habits, food habits, reproduction, and population dynamics, respectively. Where appropriate, Cattle Egrets are compared to the other ardeid species breeding in Texas with which they may, or do, come into contact. The last two sections discuss the role of the Cattle Egret in the ecosystem: the problems it faces as a result of environmental contamination and expanding human populations, as well as its economic importance.

The amount of available literature on this species makes any literature survey a gargantuan task. Even summarizing the Texas data, much of which were collected by the author, is a large undertaking. Occasionally the amount of material available proves to be too much,

and the temptation to squeeze in everything gives rise to crowded and confusing figures and maps. In some places, long lists of citations break up the text, making it difficult to follow. In other places, however, there is insufficient support for some of the statements made. For example, when discussing his own data, the author makes claims that are based on small sample sizes or that are unsubstantiated by statistical testing.

There are a number of minor instances in which poor writing style results in confusion about what is really meant. There are also some rather contradictory passages. A section starting on p. 76, for example, discusses sibling competition. Although it begins with the statement, "during extensive observations, sibling competition seemed to be minimal in Texas heronries," it goes on to discuss such competition in detail and to describe chick feeding behavior in a way that implies that sibling aggression is common. The statement, "Beak-grab feeding develops at 4–8 days after hatching, and the siblings become strongly competitive," for example, would seem to contradict the earlier remark. In addition, "starvation or cannibalism of the youngest chick" is listed as a cause of nestling mortality among Cattle Egrets.

Overall, the effort put into producing the book was well worthwhile. As an exhaustive survey of the literature and as a comprehensive summary of Cattle Egret biology, this monograph should prove invaluable not only to those interested in this species, but also to those working on other ardeids.—Nancy J. Flood.

The Birds of the Wetlands. By James Hancock. Facts on File, New York, New York, 1984:152 pp., over 120 color photos. $22.95.—The title of this attractive book is somewhat misleading. Mr. Hancock is a well-known authority on herons, and one might expect a detailed discussion of the biology of this and similar groups. However, the book turns out to be an extended travelog; in nine chapters the author takes us to single locations in North America (Everglades National Park), South America, Africa, India, China, Japan, Indonesia, Australia, and Europe (Coto Doñana). For each locality Hancock describes the area and tells of his visits there to photograph birds. Most of each chapter consists of describing the species seen. In the back of the book, complete checklists of the birds of the areas visited are given, as well as some travel hints about visiting those areas.

But as pedestrian as is most of the text, the photographs are a different story. Mr. Hancock demonstrates that he is an outstanding bird photographer, and even includes a section of photographic advice. The 120 photographs are a marvellous collection of portraits of herons, storks, ibises, waders, and other wetland species, with a few raptors thrown in. Unfortunately, the publishers adopted the abominable technique of printing a beautiful picture across the centerfold of the book. Thus a fine picture of a White-naped Crane (*Grus vipio*) has the body and most of the neck on page 71 with the head barely visible on page 70.

Throughout most of the text there is a strong conservation theme. In chapter after chapter, it is mentioned that these wild wetlands are under some kind or other of adverse pressure.

The price of the book is high for the vicarious enjoyment of the birding outings described, but the collection of pictures is well-worth having.—George A. Hall.

Ecogeographical Variation in Size and Proportions of Song Sparrows (*Melospiza melodia*). By John W. Aldrich. Ornithological Monographs No. 35, American Ornithologists' Union, Washington, D.C., 1984:134 pp. $10.50.—The appearance of a new treatment by one of American's respected taxonomists on the preeminent North American example of a polytypic species, indeed, one of the best examples of a polytypic species anywhere, is a major event. The time is right for a new look at the Song Sparrow (*Melospiza melodia*). Unfortunately, this study does not live up to its promise or to my own expectations.

"In the present study I have correlated measurements and proportions of Song Sparrows with 'Life Areas' (Aldrich 1963, 1966 [the latter reference is a published poster]), 'Ecoregion Provinces,' 'Ecoregion Sections' (Bailey 1976), and combinations of Life Areas and Ecoregion Sections, in an attempt to determine the probable adaptive value of morphological [size] variation" (p. 1; the brackets are mine). Measurements, to the nearest 0.1 mm, were made of wing chord, wing tip (tip of longest secondary to tip of longest primary), tail, culmen (total), maximum culmen depth and width, tarsus, and middle toe. A total of 826 males and 406 females collected May through August were used to avoid inclusion of migrants. Data are presented for each measured element as number of specimens, mean, and standard deviation. Data were divided by sex into 17 Life Areas (Tables 1 and 2), 23 Ecoregion Provinces (Tables 3 and 4), and 79 Ecoregion Section/Life Areas (Tables 5 and 6). In Table 5, the number of males per region ranged from 0 to 69, with 46 divisions having 10 or fewer specimens. Maps are presented summarizing each element, with an L (longer or larger), M (median one-third of group), or S (shorter or smaller) in each Ecoregion Section. Graphs present north–south and east–west transects for each element; correlation coefficients and differences between areas and their statistical significance as indicated by Student's *t*-tests are discussed.

Song Sparrows use moist edge habitats for nesting. In the East where moisture abounds, succession is rapid; thus, suitable edges are widespread but ephemeral (away from the salt marshes), and color-based subspecies are poorly developed. (There are only four races east of the Rockies.) There is essentially no variation in size. In the West moist substrates are mainly riparian, aquatic, or littoral edge habitats. Waterways are more permanent and isolated through time; subspecies based on color and size are well developed. The species occurs in relatively small patches of relatively permanent habitat, isolated from one another by largely unsuitable habitat. Thus, the fracturing of the species range into Life Areas, without regard to the local habitat and ecology, prejudices the data. Alternately, the use of phyto-ecologic subunits in the face of years of taxonomic experience showing relative morphologically homogeneous populations appears to be of little value. For example, on the southern edge of the Mexican Plateau size variation is important, but the diverse populations are combined within a single phyto-region. A map of collecting localities would have revealed that the species does not occur in central or northern Labrador, nor in Alaska away from the coastal areas. The maps, however, give the impression that the relative culmen lengths are shorter in those regions than in coastal Alaska where the species does occur!

Geographic variation in Song Sparrows primarily involves color; even in the East the subspecies are characterized by color differences. This most important character was omitted from the study.

The mensural study should have been done on specimens showing genetically, not edaphically, controlled plumage characters; i.e., on specimens in new, unworn plumage. I cannot believe that a taxonomist of Dr. Aldrich's acumen could not distinguish migrant specimens when such distinction was critical. To prove to myself the validity of my long avoidance of worn nesting-season specimens whenever possible, I measured to the nearest mm, without regard to age, the wing tip of male Song Sparrows from the Northeast from four time periods. The number of specimens measured and their means were November and December 19 (10.6), June 25 (9.2), July 24 (8.8), and August (7.9)! The difference between worn and unworn specimens is equivalent to that between males from "Arctic-Alpine (Aleutian)" (9.9), where fading would be less severe and wear is probably reduced in the less abrasive vegetation, and "Mesquite-Grassland" (7.2), i.e., Arizona where wear and fading are extreme. The mean value presented for "Eastern Deciduous Forest" was 9.1. Tail measurements are even more affected by wear (of course, this criticism is not valid for the culmen, tarsal, and toe measurements). Further, I believe that by examining feather shape and wear, most specimens could have been aged relatively reliably. There would appear to be no reason not

to use better material for resident populations. Unnumbered tables summarize all measurements by Life Areas and Ecoregion Provinces. On each table, areas are arranged in order of decreasing size of the element and, consequently, arrangements vary on every table. These tables are interesting; unfortunately, they may be accepted at face value and referred to by future textbook writers and armchair biogeographers who are unaware of the problems mentioned above.

A study of size variation in 1984 should not have attempted to do less than the now classic studies of size variation by James (Ecology 51:365–390, 1970) for a single character in relation to climate in several species, or by Power (Univ. Kans. Publ. Mus. Nat. Hist. 19:1–83, 1970) for multiple characters in a single species.

The overall conclusions of this monograph are (1) that northern, more migrant populations of Song Sparrows are larger and have longer wings with longer wing tips (southern birds are smaller) and (2) that western populations, which are more restricted to aquatic habitats, are more insectivorous and have relatively finer, more pointed bills. A competent ornithologist would have predicted this when presented with the distribution of the species and the habitat restrictions.

Four appendixes discuss or list breeding habitats (I), migration [based on banding data] (II), recoveries of winter-banded birds (III), and food (IV). The appendixes were worth publishing, but as for the text, I can only ask, why was it published? In my opinion, the study was performed using the wrong materials, did not gather the most important data, and utilized only basic (if not primitive by 1984 standards) statistical tests.—Robert W. Dickerman.

The Joy of Birding: A Guide to Better Birdwatching. By Chuck Bernstein. Capra Press, Santa Barbara, California, 1984:201 pp., line drawings. $8.95 (paper).—Mr. Bernstein likes birds, rare and common (but mostly rare), and he writes about them with great zest. If you enjoy the sport of birding, you may enjoy these numerous anecdotes of birds sought and often found.

It is Mr. Bernstein's hope that this will be an informative book. About half of the chapters are strictly anecdotal, but embedded in these are many birding tips, including clues to finding and identifying birds. In this context, faults in current North American field guides are discussed, with the National Geographic Society's recent (1983) entry emerging as least culpable.

The ornithological content of this book has to be considered "soft." The chapters that do not deal with bird trips are devoted to topics: migration, subspecies, distribution, etc. These mostly point out, with examples, that close observation of individual birds will pay off in knowledge and enjoyment. I certainly find no fault with that. But not enough is done to put such activity into a broader context of current ornithological or biological views. Such understanding would add to the enjoyment of an intelligent viewer.

There is no secret that this is a book for birders, and not for ornithologists. It may succeed in edging birders with no ornithological experience closer to being "field biologists." Individuals who occasionally or regularly slug their way through articles in The Wilson Bulletin or other ornithological journals will find nothing of scientific interest in Mr. Bernstein's book; but, on the other hand, they may find relief in the unconstrained enthusiasm that Bernstein manages to express. This book is very much "the sort of thing that people who like this sort of thing like."—Peter F. Cannell.

Bird Banding. By H. E. McClure. Boxwood Press, Pacific Grove, California, 1984:x + 341 pp., numerous figs., few tables. $15.00 (paper).—This book is intended as a manual of

practices and procedures, directed primarily at the beginning bander. Much of it was compiled in 1963, but two subsequent revisions have brought in up-to-date information from a variety of sources. The size is little larger than a field guide, making it easy to carry in the field.

The book begins with a brief history of the origins of banding around the world, comments on geological changes that may have contributed to migratory movements, and discusses the variety of types of bird movements that have been elucidated through banding and other studies.

The fourth chapter, of almost 60 pages, considers the different types of birds found around the world, the methods used to catch each type, how they may react, problems and dangers to be aware of with each, the age at which they can be banded, how they should be handled, and various other helpful hints. This would seem a most useful chapter to the beginner or to the experienced person about to extend his or her field of banding activity.

Two chapters are devoted to various types of traps and snares used to catch birds. Most of these are illustrated, and dimensions frequently are given. Regardless of the species or situation, there is a method here that would be useful. An entire chapter is devoted to the use of nets and the special problems associated with them, as well as to the simple to very elaborate ways to set nets for specific situations.

Cautions and advice about the banding of nestlings is the subject of one chapter. Nets that are set or left up at night are likely to catch bats as well as the birds for which the nets were intended. Advice and encouragement about the handling of bats is included.

Detailed lists of equipment for small banding kits or more elaborate, permanent stations are provided. An outline of the intricacies of record keeping that is essential to banding also is presented. First aid for birds, the collection of ectoparasites or blood samples, and the preservation of birds that die are considered as well.

Illustrations are numerous and very helpful. A bibliography and an index contribute to the usefulness of this volume. My criticisms are relatively minor. There are a few typographical errors; several of the illustrations printed through badly, making a few pages difficult to read; several species of owls are credited with *building* large bulky nests; and the maps in Chapter 2 seem rather obscurely related to the discussion of developing migratory pathways.

The book opens with a code of ethics for banders. Throughout the text, care in catching and handling to minimize stress on birds is emphasized. The information provided should result in the humane treatment of birds. To me the book seems a very useful guide, and a bargain at the price.—Ross James.

John Abbot in Georgia; The Vision of a Naturalist Artist (1751–ca. 1840). By Vivian Rogers-Price. Madison-Morgan Cultural Center, Madison, Georgia, 1983:149 pp., 1 color plate, 126 black-and-white plates. $15.00 (plus $2.00 postage and handling—available from the Madison-Morgan Cultural Center, 434 S. Main St., Madison, Georgia 30650.)—In conjunction with the celebration of the Georgia Semiquincentenary in 1983, the Madison-Morgan Cultural Center assembled an exhibition of the work of John Abbot. This publication is the informative catalog of that exhibition. There are black-and-white reproductions of 116 of Abbot's paintings. John Abbot is more widely known as an entomologist than an ornithologist, but it is probable that he showed Alexander Wilson several species of southern birds for which Wilson later provided the first scientific description. Several of Abbot's specimens became the types of species described by European ornithologists. Forty-five of the paintings illustrate 39 bird species. The other pictures are divided between plants and insects (primarily beetles and butterflies). The bird portraits are crude, but identifiable, being similar to those of Wilson, but the plants and insects are very good.

The catalog also includes an informative biography of Abbot and a chronology of his career as an artist and naturalist.—George A. Hall.

The Dictionary of American Bird Names, Revised Edition. By Ernest A. Choate, revised by Raymond A. Paynter, Jr. The Harvard Common Press, Boston, Massachusetts, 1985:xiv + 226 pp., several black-and-white drawings. $17.95 (cloth), $9.95 (paper).—The original edition (1973) of this book by the late Ernest Choate was reviewed in the Bulletin (87:129–130, 1975) and a more detailed review appeared in Bird-Banding (45:284–287, 1974). Both of these reviews pointed to certain flaws and errors in the lists of bird names and their meanings. This new edition incorporates numerous revisions by Raymond Paynter. Principally the changes are to incorporate the nomenclature of the 6th Edition of the A.O.U. Check-list, although the older names are still included. Paynter also has corrected the many errors that had been pointed out in the reviews. In his revisions Paynter has been successful in his attempt to keep the flavor of Choate's original style. The original edition was plagued with so many typographical errors that it left a very negative impression of the standards of the publisher. I noted a few typos in the revised edition, but in general this matter has been corrected. This edition can be recommended to anyone who wants a lexicon of bird names, but the definitive treatment still remains to be done.—George A. Hall.

Just a Lark. By Jim Flegg, Norman Arlott, Eric and David Hosking. Croom Helm, Dover, New Hampshire 03820. 1984:160 pp., 141 black-and-white photographs, 141 cartoons. $15.00.—It's a little expensive for the purpose, but this little book is certainly an amusing read for anyone. One hundred forty-one species or groups of species are discussed. There is an informative discussion of each species (by Flegg), a good photograph (by Hosking *pere et fils*), and an amusing cartoon by Arlott. The species selected are worldwide in distribution. The text is of some value and the photos are good, but small and heavily cropped. The cartoons are excellent. A Hobby (*Falco subbuteo*) equipped with binoculars and field guides, meadowlark (*Sturnella* sp.)—a boy and girl bird in cozy embrace in grassy field—well, you get the idea.—George A. Hall.

Wilson Bull., 97(4), 1985, pp. 591–605

PROCEEDINGS OF THE SIXTY-SIXTH ANNUAL MEETING

JOHN L. ZIMMERMAN, SECRETARY

The Sixty-sixth Annual Meeting of The Wilson Ornithological Society was held Wednesday, 5 June to Sunday, 9 June 1985 at the University of Colorado in Boulder, Colorado, and in joint session with the Cooper Ornithological Society for the fourth time. The meeting was sponsored by the University of Colorado, The Denver Museum of Natural History, and the Boulder Audubon Society. Cynthia Carey chaired the Local Committee on Arrangements composed of Carl Bock, Clait Braun, Bob Cohen, Alex Cruz, Becky Evans, Diane Larson, Wes Miles, Joe Ortega, Ronald Ryder, Tom Strong, Diana Tomback, and Betsy Webb.

The Council met from 08:00 to 17:00 on Wednesday, 5 June. Registration for the 222 members and guests attending opened that afternoon, and everyone enjoyed an outdoor barbecue and social on the patio of Kittredge Commons that evening. The opening session of the meeting was held Thursday morning at 08:45 in the Chemistry Building, and the scientific program was presented daily in double sessions until Saturday at 16:00. The local committee scheduled early morning field trips every day and had arranged daily guest-spouse tours to Central City, the Coors Brewery, the Broadmoor Hotel, the Air Force Academy, the Denver Art Museum, and the Colorado Heritage Center. Other special events were an evening program of slides and films on Thursday, including an outstanding multi-screen presentation by Perry Conway, a freelance natural history photographer from Boulder, and a wine and cheese reception held in the University's Memorial Center that featured the entries by amateur artists for the Sutton Award. On Wednesday afternoon the meeting of the International Council for Bird Preservation was held in the University Events Center.

On Sunday, all-day field trips were conducted to Rocky Mountain National Park, led by Clait Braun, and the Pawnee National Grasslands, led by Ron Ryder.

The annual banquet was held amid dioramas of African wildlife at The Denver Museum of Natural History. The following awards were presented:

EDWARDS PRIZE (for the best major article in volume 96 of *The Wilson Bulletin*)

J. M. Sprenkle and C. R. Blem, "Metabolism and food selection of eastern House Finches," Wilson Bull., 96:184–195.

MARGARET MORSE NICE AWARD

Andrew Balestracci, "The effects of an increasing Double-crested Cormorant population on a Great Black-backed–Herring Gull nesting colony."

LOUIS AGASSIZ FUERTES AWARDS

Gloria R. Dobush, "Use of breeding ground resources for reproduction by White-winged Scoters."

John M. Marzluff, "Social communication and recognition in Pinyon Jays."

PAUL A. STEWART AWARDS

Carola A. Haas, "Site fidelity and dispersal of birds in a patchy environment."
Geoffrey E. Hill, "The reproductive consequences of subadult plumage in male Black-headed Grosbeaks."
Wendy M. Jackson, "Kleptogamy and kleptogamy-avoidance mechanisms in a polyandrous and monogamous jacana."
Frank J. Joyce, "Nest site selection by three passerines associates of Hymenoptera in Central American dry forest."
Mark J. Kasprzyk, "Significance of migratory stopovers for Semipalmated Sandpipers."
Lisa H. MacIvor, "Foraging success of the Bonaparte's Gull: energetics and interaction with prey."

ALEXANDER WILSON PRIZE (for best student paper at the meeting)

Paul Hendricks, University of Montana, "Foraging ecology of alpine-nesting Water Pipits."

GEORGE M. SUTTON AWARD

Karen Allaben-Confer
Jonathon Alderfer—Honorable mention

FIRST BUSINESS MEETING

The first business meeting was held at 09:00 on Thursday, 6 June with President Jerome A. Jackson presiding. Those appointed to the auditing committee were announced. Secretary Zimmerman summarized the highlights of Wednesday's Council meeting, including the report of the nominating committee chaired by George Hall (with A. S. Gaunt and Richard Conner as members). It was also reported that Keith Bildstein was reelected Editor of *The Wilson Bulletin,* and that Life memberships will be increased to $400 effective in 1987. Elliott Tramer is chairman of the Centennial Committee, and the secretary reported that the Council had voted to provide a Centennial Fund to which members can contribute to assist the Society for the 1988 meeting. Lastly, the secretary read the names of members who had died in the past year—H. E. Clements (Fairport, NY), John H. Foster (Wayne, PA), W. W. H. Gunn (Bobcaygeon, ONT), Rodolphe Meyer de Schauensee (Devon, PA), Demund W. Mudge, Jr. (Dallas, TX), George W. North (Burlington, ONT), and C. Brooke Worth (Delmont, NJ)—while the assembled members stood in their honor.

Robert D. Burns then gave the treasurer's report.

REPORT OF THE TREASURER
1 January 1984 to 31 December 1984

GENERAL FUNDS

RECEIPTS		
Dues collected in 1984		
Regular Memberships for 1984	$ 20,312.03	
For 1985	15,952.00	
Sustaining Memberships for 1984	315.00	
Student Memberships for 1984	2,987.25	
For 1985	1,434.00	
Family Memberships for 1984	407.50	
For 1985	416.00	
TOTAL DUES		$ 41,823.78
Subscriptions to *The Wilson Bulletin*		
For 1984	$ 7,950.50	
For 1985	1,777.75	
TOTAL SUBSCRIPTIONS		$ 9,728.25
Back Issues of *The Wilson Bulletin*		$ 1,601.00
Interest and Dividends		$ 22,639.61
Royalties		$ 1,776.99
Contributions from Authors		$ 1,999.00
Contributions to the Student Awards Funds		$ 1,096.00
Contributions to Endowment and Life Memberships		$ 3,935.00
TOTAL RECEIPTS—1 Jan.–31 Dec. 1985		$ 84,599.63
DISBURSEMENTS		
The Wilson Bulletin		
December 1983	$ 15,862.39	
March 1984	11,484.32	
June 1984	13,158.20	
September 1984	11,869.14	
Colorplates	3,107.95	
Editorial Expenses Barlow	5,950.00	
Editorial Expenses Bildstein	2,356.72	
TOTAL PRODUCTION COSTS		$ 63,788.72
OSNA Expenses		$ 13,759.33
Deposit of Student Award Contributions to Dreyfus Liquid Assets		$ 1,096.00
Deposit to Student Award Accounts from Endowment		$ 2,900.00
Dues to International Council for Bird Preservation 1984		$ 100.00
Travel Reimbursement for Editors		$ 773.99
Postage, Officers, and Back Issue Mailings		$ 270.00
Treasurer's Bond		$ 51.00
Refunds		$ 15.00
Balance of 1978 Van Tyne Library Funds sent to Van Tyne Library		$ 562.32
Expenses over income of 1984 Annual Meeting		$ 325.83
TOTAL DISBURSEMENTS—1 Jan.–31 Dec. 1984		$ 83,641.19
1984 Income over Expenses		$ 958.44

CASH ACCOUNTS

Checking Account, Peoples Bank, Gambier, OH, 31 Dec. 1984	$ 6,412.43	
Savings Account, 31 Dec. 1984	212.43	
Dreyfus Liquid Assets, 31 Dec. 1984	39,790.57	
TOTAL CASH ON HAND		$ 46,415.43

DESIGNATED ACCOUNTS

LOUIS AGASSIZ FUERTES RESEARCH FUND

RECEIPTS	
Endowment Earnings	$ 450.00
DISBURSEMENTS	
David Lemmon	$ 450.00

ALEXANDER WILSON PRIZE

RECEIPTS	
Endowment Earnings	$ 100.00
DISBURSEMENTS	
Peter Frederick	$ 100.00

ERNEST P. EDWARDS PRIZE

RECEIPTS	
E. P. Edwards	$ 150.00
DISBURSEMENTS	
John L. Zimmerman	$ 150.00

PAUL A. STEWART AWARDS

RECEIPTS	
Endowment Earnings	$ 1,800.00
DISBURSEMENTS	
Eric K. Bollinger	$ 300.00
Paul E. Kendra	300.00
Cynthia Ann Staicer	300.00
Mark A. Stern	300.00
Tom C. Will	300.00
Ann Marie Wyckoff	300.00

STUDENT MEMBERSHIP AWARDS

RECEIPTS	
Endowment Earnings	$ 224.00
DISBURSEMENTS	
16 Student Memberships Awarded	$ 224.00

ANNUAL MEETING RESERVE FUND

1983 Balance	$ 229.00
1984 Expenses over Income	325.83
1984 Balance	(96.83)

ENDOWMENT[a]

Value of Endowment Fund, 31 Dec. 1983, at cost	$198,791.58
Losses due to Sales of Bonds	2,065.38

Value of Endowment Fund 31 Dec. 1984, at cost	$196,726.20
Earnings from Endowment Fund for 1984	$ 22,639.61

[a] Account 20-05-001-7150567 Mellon Bank (Central) N.A., formerly—The Central Counties Bank, State College, PA.

The Editor's report was presented by Keith L. Bildstein. Summaries of the reports of Jon C. Barlow and Keith L. Bildstein are presented below.

EDITORS' REPORTS—1984

Volume 96 (1984) of *The Wilson Bulletin* was the largest in the history of the Society and contained 775 numbered pages. The December 1984 issue was the largest single issue ever published by the Society at 261 numbered pages. The editorial offices received 25 major articles and 28 notes between 1 January and 15 May 1984. The latter is the date after which all manuscripts received by me (except five) were sent on to Editior-elect Keith Bildstein.

Again I thank everyone who made my seven-year tenure as Editor a pleasant one. I'm pleased to have been able to serve my colleagues and profession in so rewarding a manner.

Jon C. Barlow, *Retired Editor*

On 15 May 1984 I assumed the duties of Editor of *The Wilson Bulletin* beginning with Volume 97 (1985). Since then I have received 135 manuscripts (over an 11-month period through 15 April 1985). Forty-eight of the mss were submitted as Major Papers, 87 were submitted as General Notes. Of these, 29% have been accepted for publication, 23% have been rejected, 27% have been returned to authors for revision, and 21% are currently being reviewed by referees. The 77 mss received in 1984 were returned to their authors 98 ± 32 days after their receipt. I hope to reduce this turn-around time by adding to the list of referees who are willing to review papers without advance notice. There are plans for color plates for all issues in 1985, as well as for the first issue in 1986. The March 1985 issue was published in mid-April. The June 1985 issue will be published no later than mid-July, and the September 1985 issue should be published on time in September.

I have received essential assistance from many people in the Editorial Office and elsewhere. Jon Barlow, Margaret May, and Janet Mannone, as well as the staff at Allen Press, helped to make my assumption of the editorship a smooth one. Others that I thank for outstanding service include: Associate Editors, M. W. Collopy, R. N. Conner, J. P. Myers, W. M. Shields, and J. R. Walters; Assistant Editors, A. E. Conway, E. J. Hawfield, J. A. Hovis, J. W. Johnston, J. B. Olson, and D. L. Rankin; Review Editor, G. A. Hall; Color Plate Editor, W. A. Lunk; Index Editor, K. G. Beal; and numerous members of The Wilson Society, including S. Gaunt, A. Gaunt, and J. Jackson. I also thank the 165 volunteer referees who reviewed mss for *The Wilson Bulletin* during the past 11 months.

Keith L. Bildstein, *Editor*

SECOND BUSINESS MEETING

President Jackson called the second business meeting to order at 13:20 on Saturday, 8 June. Chairman Zernickow presented the report of the Auditing Committee:

We, the undersigned, have reviewed the records presented by the Treasurer covering the

period of 1 January 1984 to 31 December 1984 with the intent of verifying that the records correctly reflect the assets of the Society and the correct and timely posting of income and expenditures during this period. We found no errors and are satisfied that the financial report of the Treasurer correctly reflects the financial health of the Society. Further, we commend Dr. Robert D. Burns for his excellent work in carrying out his responsibilities in an exemplary fashion both for the current year and for the long range financial health of the Society.

William A. Klamm, *member*
Robert A. Whiting, *member*
Hubert P. Zernickow, *chairman*

The move to accept the report of the Auditing Committee was made by Clait Braun, seconded by Helmut Mueller, and passed by the membership.

The Report of the Nominating Committee was presented by Chairman Hall. It was moved by Thomas Vawter and seconded by Kathleen Anderson that the following slate of officers be elected by acclamation. The motion passed. For 1985–1986: President, Clait E. Braun; First Vice-President, Mary H. Clench; Second Vice-President, Jon C. Barlow; Secretary, John L. Zimmerman; Treasurer, Robert D. Burns; Council Member (term to expire in 1987), Curtis S. Adkisson; Council Member (term to expire in 1988), Richard B. Stiehl.

New Members of The Wilson Society were formally elected to membership through the motion of Elliot Tramer, seconded by Glen Woolfenden, and passed by the membership.

Nancy Mueller presented the report of the Resolutions Committee (Jim Tate, chairman).

REPORT OF THE RESOLUTIONS COMMITTEE

RECOGNIZING, that the Cheyenne Bottoms Wildlife Area of central Kansas is an outstanding marshland habitat with extraordinary wildlife values, and

RECOGNIZING, that the marshland is used by endangered species, such as Peregrine Falcons, Bald Eagles, and Whooping Cranes, and

RECOGNIZING, that the area is traditionally used by millions of shorebirds, marshbirds, and waterfowl each season, and

RECOGNIZING, that these numbers of shorebirds are of international significance as they represent the greatest concentration east of the 105th longitudinal line, and

WHEREAS, other wetland areas in the Great Plains are rapidly disappearing, and

WHEREAS, streamflows throughout the western Great Plains are decreasing and many are threatened by agricultural and municipal uses, and

WHEREAS, state agencies are currently launching a feasibility study of how to save this critical wetland habitat,

THEREFORE BE IT RESOLVED that the Cooper and Wilson Ornithological societies urge the responsible agencies to work vigorously to protect the habitat for all migratory bird resources, and

THEREFORE BE IT FURTHER RESOLVED that the Cooper and Wilson Ornithological societies strongly urge the responsible agencies to consider all possibilities for obtaining, holding, and using the available water resources at Cheyenne Bottoms in a more effective manner to protect the usage of the area by migratory bird resources.

Glen Woolfenden moved, and Helen Lapham seconded, to accept this resolution. The motion passed.

WHEREAS, Alexander Wilson is known to ornithologists as the Father of American Ornithology, and in the last decade before his untimely death in 1813 at the age of 47, wrote

the text of his *American Ornithology* and completed 76 hand colored plates depicting more than 300 individual birds, and

WHEREAS, according to his biographer, George Ord, Alexander Wilson once expressed a desire to be "buried in some rural spot sacred to peace and solitude where the charms of nature might invite the steps of the votary of the muses and the lover of science, and where birds might sing over his grave," and

WHEREAS, Alexander Wilson's grave site at Gloria Dei (Old Swede's) Church in Philadelphia has fallen into disrepair, and efforts are now being made to repair the original marker and brick walkway surrounding it and to plant the area with shrubs attractive to birds,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society enthusiastically supports the efforts of the Scottish Historic and Research Society and other concerned citizens of Philadelphia to help fulfill Alexander Wilson's wishes through the restoration and plantings.

Richard Banks moved, and John Zimmerman seconded, to accept this resolution. The motion passed. It was pointed out by President Jackson that the Council had voted to contribute $200 towards this project, and members are encouraged to support this effort in spirit as well as financially. Contributions in the name of the Society should be sent to the Treasurer.

WHEREAS, the Cooper and Wilson Ornithological societies held their fourth joint meeting from 5–9 June 1985 at Boulder, Colorado, at the invitation of the University of Colorado, the Denver Museum of Natural History, and the Boulder Audubon Society, and

WHEREAS, the local Committee, chaired by Dr. Cynthia Carey, arranged varied and stimulating activities, including excellent food and drink, accommodations, evening programs, and field trips, and

WHEREAS, the scientific program committee, chaired by Drs. Carl E. Bock and Mary H. Clench, assembled an outstanding slate of stimulating technical papers,

THEREFORE BE IT RESOLVED that the Cooper and Wilson Ornithological societies extend sincere appreciation to all those organizations and individuals who worked so diligently to make this a successful and stimulating meeting.

It was moved by Helmut Mueller and seconded by Ralph Schreiber to accept this resolution. Motion passed.

President Jackson thanked the members of the Society for their cooperation during his two-year tenure. Richard Banks moved, and Clait Braun seconded, to adjourn the meeting. Motion passed.

The reports of the standing committees were given as follows:

REPORT OF THE COMMITTEE ON STUDENT MEMBERSHIPS—1984

A total of 209 letters was sent to selected members of The Wilson Ornithological Society who were in positions that afforded the identification of students eligible for the Student Membership Awards provided by the Society. In addition to a set of application materials, a form was provided on which members could list the names of students who were not being nominated for an award but who should be sent information regarding student membership in the Society. Announcements of the availability of these awards were also made in *The Wilson Bulletin* and in the *Ornithological Newsletter.* Application materials were sent in response to 18 letters of inquiry that were probably generated by these announcements.

Completed applications were received from 31 nominees. Members also provided the names of 14 students to whom an invitation to join the Society was sent. As in the past,

two criteria were used by the committee in the evaluation: (1) the applicant's demonstrated commitment to ornithology and (2) the expectation for a long-term professional involvement in ornithology. Twenty-nine candidates qualified. Their names and schools are listed below:

Jean V. Adams, Bradley Univ.; Terry Armstrong, Queen's Univ.–Ontario; James F. Bergan, Texas Tech. Univ.; Reed Bowman, MacDonald College; Michael W. Brown, Iowa State Univ.; David G. Cook, Texas Tech. Univ.; Thomas I. Crossman, Univ. Connecticut; Clyde D. Cummins, Miami Univ.; Tristan J. G. Davis, Louisiana State Univ.; Barrett A. Garrison, Virginia Polytechnic Institute and State Univ.; Joseph A. Gubanyi, Univ. Nebraska; Danny J. Ingold, Mississippi State Univ.; Walter N. Johnson, Univ. Maine; Nedra K. Klein, Louisiana State Univ.; Natasha C. Kline, Univ. Miami; Jacqueline J. Lape, North Carolina State Univ.; David Lemon, Univ. Toledo; Mei-yao C. Louis, Univ. Minnesota–Duluth; Richard W. Lundquist, Univ. Washington; Sarah J. Madsen, Univ. Washington; D. James Montjoy, Queen's Univ.–Ontario; David C. Morimoto, Boston Univ.; Cecilia M. Riley, Univ. Arkansas; BethAnn Sabo, George Mason Univ.; Virginia M. Scarpino, State Univ. New York–Geneseo; John M. Shipley, Jr., Idaho State Univ.; Douglas G. Sheeley, Texas Tech. Univ.; Stefen Sobkowiak, MacDonald College–Quebec; Kimberly A. With, San Francisco State Univ.

It was particularly gratifying that there were four undergraduates among those receiving Student Membership Awards. Unsuccessful student award nominees were sent letters inviting them to join the Society.

Richard N. Conner, *Chairman*

MEMBERSHIP COMMITTEE REPORT—1984

The total paid membership in the Society was 2706 as of 14 April 1985. Two hundred and one new members joined the Society this past year. My office handled 62 new membership requests. Of these, 34 came from membership brochures, 4 from the ONSA Newsletter, 4 from *The Wilson Bulletin* mailing cover, and 20 from miscellaneous sources. The remaining originated from "dues notice" and were handled completely by ONSA. I predict that the revision of the "Membership Inquiries" notice on the inside back cover of *The Wilson Bulletin* in Volume 96(1), will increase the number of requests I will handle. The display board and membership brochures are available for local meetings. Anyone wishing brochures or use of the display board is encouraged to contact me.

Richard Stiehl, *Chairman*

LIBRARY COMMITTEE REPORT—1984

The calendar year 1984 was another satisfactory, if not particularly outstanding, one for the Josselyn Van Tyne Memorial Library. Our Society membership continued its use of the facility and its fine cooperation in helping to augment it. Janet Hinshaw continued to handle our affairs most capably.

Loans of 160 items were made to 51 members in 80 separate transactions during the year.

Donations of 473 items (including 18 books, 170 reprints, 219 journal issues, 65 reports and pamphlets, 2 theses, and 1 translation) came from 22 individuals. These were: M. Bechard, B. G. Beddall, A. J. Berger (207 items, or some 44% of the total), F. Evans, S. Fefer, N. L. Ford, J. Gapycznyski, S. M. Goodman, J. Haffer, J. Hinshaw, W. Hoffman, S. Holohan, F. E. Lohrer, H. Mayfield, D. McWhirter, T. Miley, S. Nesbitt, R. B. Payne, A. C. Simon, W. Southern, R. W. Storer, T. Van't Hof, J. D. Webster, and Col. L. R. Wolfe.

From the New Book Fund, 16 new books were purchased; to it was added a total of $400

from the sale of 20 duplicate books and journals. Approximately 500 journal issues from our stock of duplicates were traded with other libraries for those needed to fill gaps.

Through 119 exchanges of *The Wilson Bulletin* we received 157 journals, books, and reprints. Thirty-one gifts (40 titles) and 7 subscriptions (10 titles) raised to 207 our total of journals and other items currently received.

There were declines, from last year's totals, in a number of categories, most notably in donations received. Some of these are easily explained, and probably there is no overall drop in member support for the library. We continue to hope, however, for an increase.

William A. Lunk, *Chairman*

PAPERS SESSION

The scientific papers sessions were arranged by Carl E. Bock and Mary H. Clench. Individual sessions were chaired by Clait Braun, Alexander Cruz, Frank B. Gill, Douglas B. Inkley, J. P. Myers, Kenneth C. Parkes, Richard T. Reynolds, Peter C. Stacey, Stanley A. Temple, Diana F. Tomback, Jared Verner, and Carol M. Vleck.

David S. Lee and Mary K. Clark, North Carolina State Museum of Natural History, Raleigh, NC, "Summer food, molt, weights, mercury loads, and activity patterns of American Swallow-tailed Kites."

Brian D. Linkhart, Dept. Fishery and Wildlife Biology, Colorado State University, Ft. Collins, CO; Richard T. Reynolds, Rocky Mtn. Forest and Range Expt. Station, Ft. Collins, CO; and Ronald A. Ryder, Dept. Fishery and Wildlife Biology, Colorado State University, Ft. Collins, CO, "Size, spacing, and utilization of breeding territories by Flammulated Owls."

Robert D. Ohmart, William C. Hunter, and Bertin W. Anderson, Center for Environmental Studies, Arizona State University, Tempe, AZ, "We are out of the woods and so are the birds."

David L. Fischer, Dept. Zoology, Brigham Young University, Provo, UT, "Ranging behavior of Cooper's Hawk (*Accipiter cooperii*) and Sharp-shinned Hawk (*A. striatus*) in Utah."

George T. Allen, Zoology Dept., North Dakota State University, Fargo, ND, "Estimation of the nesting populations of Prairie Falcons (*Falco mexicanus*) and Golden Eagles (*Aquila chrysaetos*) in North Dakota."

D. A. Palmer, Dept. Fishery and Wildlife Biology, Colorado State University, Ft. Collins, CO, "Microhabitat segregation patterns between two species of the genus *Aegolius* in north-central Colorado."

John M. Marzluff, Dept. Biological Sciences, Northern Arizona Uiversity, Flagstaff, AZ, "Do Pinyon Jays have friends?"

D. Arch McCallum, Dept. Biology, University of New Mexico, Albuquerque, NM, and D. C. Bolster, Cottonwood Gulch Foundation, Thoreau, NM, "An experimental study of intraflock dispersion in the Mountain Chickadee."

T. David Pitts, Biology Dept., University of Tennessee, Martin, TN, "Size and organization of Eastern Bluebird flocks in Tennessee."

Stephen Pruett-Jones and Melinda Pruett-Jones, Dept. Biology, University of California at San Diego, La Jolla, CA. "Home range and use of space in Lawes' Parotia: a frugivorous, lek-mating bird of paradise."

Doris J. Watt, Dept. Biology, Saint Mary's College, Notre Dame, IN, "Selfish site selection in roosting tropical birds."

Michael R. Conover, Dept. Plant Pathology and Ecology, Connecticut Agric. Expt. Sta., New Haven, CT, "Passive mobbers and the cultural transmission of predator information in gull colonies."

Tex A. Sordahl, Biology Dept., Luther College, Decorah, IA, "On the occurrence of predator-mobbing in shorebirds."

Wesley W. Weathers, Dept. Avian Sciences, University of California, Davis, CA, "Thermal correlates of the Blue-black Grassquit's unique display."

Carol M. Vleck, Dept. Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, "Nesting season and reproductive hormones in a Sonoran Desert bird, the Curve-billed Thrasher."

Guy A. Baldassarre, Dept. Zoology-Entomology, Auburn University, Auburn, AL, "Changes in body weight and carcass composition of non-breeding Green-winged Teal on the southern high plains of Texas."

Cynthia Carey, Dept. EPO Biology, University of Colorado, Boulder, CO; F. Leon-Velarde, G. Castro, and C. Monge, Universidad Peruana Cayetano Heredia, Lima, Peru, "Adaptation of avian eggs to high altitudes in the Peruvian Andes."

John S. Kirkley, Dept. Biology, Utah State University, Logan, UT, "Heat stress and the water budget of nestling Swainson's Hawks."

Sheila A. Mahoney, Dept. Biological Sciences, Florida Atlantic University, Boca Raton, FL, and Joseph R. Jehl, Jr., Hubbs-Sea World Research Inst., San Diego, CA, "Avoidance of salt-loading by birds inhabiting an alkaline lake."

Charles R. Blem, Dept. Biology, Virginia Commonwealth University, Richmond, VA, "Mathematical prediction of lipid depots in small birds."

J. W. Hupp, Dept. Fishery and Wildlife Biology, Colorado State University, Ft. Collins, CO, "Spring changes in lipid reserves of adult male Sage Grouse."

B. S. Obst, Dept. Biology, University of California, Los Angeles, CA, "Wax digestion in Wilson's Storm-Petrel (*Oceanites oceanicus*)."

Jeffrey D. Brawn, Dept. Biological Sciences, Northern Arizona University, Flagstaff, AZ, "Experimental analyses of density and habitat effects on the breeding biology of Western Bluebirds."

Terry Root, Biology Dept., Princeton University, Princeton, NJ, "Continent-wide examination of distribution and abundance patterns."

J. J. Rotella, Program in Wildlife Biology, Washington State University, Pullman, WA, "A test of the assumed relationship between population density and number of birds vocalizing."

Cynthia Staicer, Cabo Rojo National Wildlife Refuge, Boqueron, PR, "Spacing behavior of migrant and resident warbler species in winter in southwestern Puerto Rico."

Michael L. Avery and Charles Van Riper III, CPSU, National Park Service, Wickson Hall, University of California, Davis, CA, "Year-to-year changes in winter bird population levels at Pinnacles National Monument, California."

David F. DeSante, Point Reyes Bird Observatory, Stinson Beach, CA, "A field test of the variable circular-plot censusing technique in a Sierran subalpine forest breeding bird community."

Robert B. Hamilton, School of Forestry, Wildlife, and Fisheries, Louisiana State University, Baton Rouge, LA, and G. D. Lester, Louisiana Natural Heritage Program, DNR/CMD, P.O. Box 44124, Baton Rouge, LA, "Sample size requirements for computing diversity in a mixed pine-upland hardwood forest in central Louisiana."

Douglas B. Inkley and Stanley H. Anderson, Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, WY, "Species richness patterns of birds in North America."

S. D. Schemnitz and T. D. Potter, Dept. Fishery and Wildlife Sciences, New Mexico State University, Las Cruces, NM, "Status and ecology of Gould's Turkey in the United States."

John L. Zimmerman and Elmer J. Finck, Div. Biology, Kansas State University, Manhattan, KS, "Disturbance frequency and population stability."

V. L. St. Louis and J. C. Barlow, Dept. Zoology, University of Toronto, Toronto, ONT, "Genetic differences between introduced Illinois and ancestral *Passer montanus*."

Richard C. Banks, U.S. Fish and Wildlife Service, Washington, D.C., "Identification of Willow and Rock Ptarmigan (*Lagopus lagopus* and *L. mutus*) by wing formula differences."

Ned K. Johnson, Museum of Vertebrate Zoology, University of California, Berkeley, CA, and Robert M. Zink, Museum of Zoology, Louisiana State University, Baton Rouge, LA, "Genetic evidence for the relationships among Red-eyed, Yellow-green, and Chivi vireos."

J. W. Hardy, Florida State Museum, University of Florida, Gainesville, FL, and T. A. Parker III, Museum of Zoology, Louisiana State University, Baton Rouge, LA, "Comments on the systematics and behavioral ecology of New World thrushes based on vocalization."

Kenneth C. Parkes, Carnegie Museum of Natural History, Pittsburgh, PA, and George A. Hall, Chemistry Dept., West Virginia University, Morgantown, WV, "What is xanthochroism?"

Stephen I. Rothstein and Robert C. Fleischer, Dept. Biological Sciences, University of California, Santa Barbara, CA, "Dialects and biogeographic patterns of range extension in western cowbirds."

G. F. Shields, Inst. Arctic Biology, University of Alaska, Fairbanks, AK, and Allan C. Wilson, Dept. Biochemistry, University of California, Berkeley, CA, "Relationships of Canada Geese (*Branta canadensis*) as inferred from restriction endonuclease analysis of mitochondrial (mt) DNA."

James R. Philips, Math/Science Division, Babson College, Babson Park, MA, "Bird-louse-fly-mite associations."

Joel Cracraft, Field Museum of Natural History, Chicago, IL, "Monophyly and phylogenetic relationships of the Pelecaniformes."

C. H. Trost and Cheryl Webb, Dept. Biology, Idaho State University, Pocatello, ID, "The effects of nest position and brood reduction on dominance and survival in young Black-billed Magpies (*Pica pica*)."

Peter B. Stacey, Dept. Life Sciences, Indiana State University, Terre Haute, IN, "Helping in the Acorn Woodpecker: ecological constraints or mutualism?"

Steven R. Beissinger, School of Natural Resources, University of Michigan, Ann Arbor, MI, "Mate desertion and reproductive effort in the Snail Kite."

Robert R. Cohen, Dept. Biology, Metropolitan State College, Denver, CO, "First-come, first-served: mate and nest-site selection by returning successful breeders of a nest-box Tree Swallow population."

Raleigh J. Robertson and D. Leffelaar, Dept. Biology, Queen's University, Kingston, ONT, "Division of labor and the implications for the mating system in Tree Swallows (*Tachycineta bicolor*)."

Robert W. Butler, Canadian Wildlife Service, Box 340, Delta, BC, "Age-related mimicry in Tree Swallows (*Tachycineta bicolor*)."

Mary V. McDonald, Dept. Zoology, University of Florida, Gainesville, FL, "Functions of female vocalizations in Scott's Seaside Sparrows (*Ammodramus maritimus peninsulae*)."

Glen E. Woolfenden, Dept. Biology, University of South Florida, Tampa, FL, and John W. Fitzpatrick, Field Museum of Natural History, Chicago, IL, "Components of lifetime reproductive sucesss in the Florida Scrub Jay."

Michael H. Tove, Dept. Biology, Utah State University, Logan, UT, "Song structuring by House Wrens."

James N. M. Smith, K. Glenna Stewart, Ian G. McClean, and David M. G. Newell, Dept. Zoology, University of British Columbia, Vancouver, BC, "Variable breeding dispersion in the American Robin."

David E. Blockstein, Bell Museum of Natural History, Dept. Ecology and Behavioral Biology,

University of Minnesota, Minneapolis, MN, "Site fidelity and reuse of nests by Mourning Doves (*Zenaida macroura*)."

R. R. Hitchcock and Ralph E. Mirarchi, Dept. Zoology-Entomology and Alabama Agric. Expt. Sta., Auburn University, Auburn, AL, "Dispersal movements of recently-fledged Mourning Doves (*Zenaida macroura*) from nest sites."

Ann Marie Wyckoff, Dept. Biology, University of North Dakota, Grand Forks, ND, "Fidelity in Chestnut-collared Longspurs (*Calcarius ornatus*) in an eastern population."

D. Westmoreland, Dept. Animal Ecology, Iowa State University, Ames, IA, "Incubation continuity and the advantage of cryptic egg coloration in open-nesting birds."

Kenneth M. Giesen and Clait E. Braun, Colorado Division of Wildlife, Ft. Collins, CO, "Demography of White-tailed Ptarmigan (*Lagopus leucurus*) in Rocky Mountain National Park, Colorado."

Brian S. Cade, Dept. Fisheries and Wildlife Biology, Colorado State University, Ft. Collins, CO, "Habitats preferred by Blue Grouse (*Dendragapus obscurus*) during winter and their spatial relation to breeding areas."

William R. Eddleman, Wyoming Cooperative Res. Unit, Box 3166, University Station, University of Wyoming, Laramie, WY, "Habitat use patterns of American Coots during fall migration in Oklahoma."

Michael L. Morrison, I. C. Timossi, and K. A. With, Dept. Forestry and Resource Mgmt., University of California, Berkeley, CA; and P. N. Manley, Dept. Wildlife Manage., Humboldt State University, Arcata, CA, "Use of tree species by forest birds during winter and summer."

John P. Kelly, Dept. Wildlife Manage., Humboldt State University, Arcata, CA, "Habitat use by riparian forest birds in the Eel River Delta, California."

D. J. Ingold, Dept. Biological Sciences, Mississippi State University, Mississippi State, MS, "A study of cavity site parameters in a guild of hole-nesting birds in the Colorado Rockies."

Richard N. Conner and K. A. O'Halloran, Southern Forest Experiment Sta., USDA Forest Service, Nacogdoches, TX, "A comparison of Red-cockaded Woodpecker (*Picoides borealis*) cavity trees in east Texas."

Jerome A. Jackson and B. J. S. Jackson, Dept. Biological Sciences, Mississippi State University, Mississippi State, MS, "Why do Red-cockaded Woodpeckers require old trees?"

Alexander Cruz, EPO Biology, University of Colorado, Boulder, CO, and James W. Wiley, Puerto Rico Field Section, USFWS, Palmer, PR, "The loss of egg-rejection behavior in the Village Weaver (*Ploceus cucullattus*) on Hispaniola."

Ralph W. Schreiber and Elizabeth A. Schreiber, Los Angeles County Museum, Los Angeles, CA, "Something about the Southern Oscillation."

Tammie K. Nakamura and Alexander Cruz, EPO Biology, University of Colorado, Boulder, CO, "Comparative nesting biology of introduced finches in southwestern Puerto Rico."

T. Y. Wang and C. J. Pei, Inst. Biology, Taiwan Normal University, Taipei, Taiwan, "A preliminary study on the breeding behavior of the Formosan Whistling Thrush."

Frank A. Pitelka, Dept. Zoology, University of California, Berkeley, CA, "Levels of analysis in research on avian lekking systems."

J. K. Gutzwiller and S. H. Anderson, Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, WY, "Simultaneous and sequential use of snags and limbs by breeding cavity-nesting birds."

J. P. L. Savard, Canadian Wildlife Service, P.O. Box 340, Delta, BC, "Use of nest boxes by Barrow's Goldeneye and American Kestrels in the aspen parkland of British Columbia."

Harlo H. Hadow, Dept. Biology, Coe College, Cedar Rapids, IA, "Hoffman's Woodpeckers back into nest cavities."

L. Barrie-Hunt and Shirley F. Hunt, Zoology Dept., Eastern Illinois University, Charleston, IL, "Hole-site selection by saguaro-excavating woodpeckers."

S. B. Gaines, School of Biological Sciences, University of Nebraska, Lincoln, NE, "Tests of three foraging hypotheses for wintering American Tree Sparrows (*Spizella arborea*)."

P. Hendricks, Dept. Zoology, University of Montana, Missoula, MT, "Foraging ecology of alpine-nesting Water Pipits."

Russell P. Balda and John Mazluff, Northern Arizona University, Flagstaff, AZ, and Glen E. Woolfenden, University of South Florida, Tampa, FL, "Food-caching behavior by the Black-billed Magpie in an urban setting at the 1985 Cooper-Wilson meeting."

Frank B. Gill, Academy of Natural Sciences, Philadelphia, PA, "Three hermits and a *Heliconia*: the coevolutionary cliff."

Kenneth L. Petersen and Louis B. Best, Dept. Animal Ecology, Iowa State University, Ames, IA, "Diet composition of nestling Sage and Brewer's sparrows in an Idaho sagebrush community."

C. John Ralph, U.S. Forest Service, Redwood Sciences Laboratory, 1700 Bayview Dr., Arcata, CA, "Life history adaptations of native Hawaiian nectar specialists."

Lester L. Short, American Museum of Natural History, New York, NY, and Jennifer F. M. Horne, National Museums Kenya, Nairobi, Kenya, "Feeding strategies of Pallid and Lesser Honeyguides at artificial beeswax sites."

Diana F. Tomback and K. L. Burnell, Dept. Biology, University of Colorado, Denver, CO, "Foraging preferences of Clark's Nutcrackers: predictions and preliminary data."

Wayne Trivelpiece and Susan Trivelpiece, Point Reyes Bird Observatory, Stinson Beach, CA, "Foraging behavior of Gentoo and Chinstrap penguins as determined by new radiotelemetry techniques."

Joseph R. Jehl, Jr., Hubbs-Sea World Research Institute, 1700 South Shores Rd., San Diego, CA, "Aspects of the fall migration of Eared Grebes: does physical fitness equal genetic fitness?"

J. P. Myers, G. Castro, J. L. Maron, E. Ortiz, M. Sallaberry, C. T. Schick, and E. Tabilo, Academy of Natural Sciences, Philadelphia, PA, "Circumcontinental migration by Sanderlings (*Calidris alba*)."

A. J. Erskine, Canadian Wildlife Service, Sackville, NB, "The changing patterns of Brant (*Branta bernicula*) migration in eastern North America."

Walter K. Taylor, Dept. Biological Sciences, University Central Florida, Orlando, FL, and Mark A. Kershner, Dept. Biological Sciences, Mississippi State University, Mississippi State, MS, "Bird casualties at the vehicle assembly building (VAB), Brevard County, Florida."

Stanley A. Temple, Dept. Wildlife Ecology, University of Wisconsin, Madison, WI, "Predicting avian response to forest fragmentation."

Elliot J. Tramer, Dept. Biology, University of Toledo, Toledo, OH, "Dredge spoil enclosures: effects on aquatic birdlife."

Charles Collins, Dept. Biology, California State University, Long Beach, CA. "Philopatry in the California Least Tern: management implications."

F. L. Knopf, Denver Wildlife Research Center, Ft. Collins, CO, "Changing landscapes and the cosmopolitanism of the eastern Colorado avifauna."

Emil K. Urban, Dept. Biology, Augusta College, August, GA, "Status of cranes in Africa in 1984."

ATTENDANCE

ALABAMA: *Auburn,* Guy Baldassarre, Ralph Mirarchi.

ARIZONA: *Green Valley,* Jack von Bloeker; *Flagstaff,* Russell Balda, Jeff Brawn, John Marzluff; *Portal,* Charles Schaughency, Mildred Schaughency; *Tempe,* Bob Ohmart; *Tucson,* Rick Bowers, John Dunning, Jr., Donald Lamm, Laurie McKean, Ruth Ogden, Steven Russell, Robert Tweit, Carol Vleck; *Williams,* James Griffing.

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REPUBLIC OF CHINA: *Taipei,* Yin Wang.

1986 ANNUAL MEETING

The Sixty-seventh Annual Meeting of The Wilson Ornithological Society will be held in Gatlinburg, Tennessee, 17–20 April 1986 under the sponsorship of the Knoxville Chapter of the Tennessee Ornithological Society. David Pitts is chairing the Local Arrangements Committee. His address is Dept. Biology, Univ. Tennessee, Martin, Tennessee 38238.

CHANGES IN FORMAT

In consultation with the Publications Committee, I have decided to revise the format of Major Papers and General Notes appearing in *The Wilson Bulletin.* The changes indicated below are effective immediately.

Authors submitting Major Papers should include an abstract rather than a summary in their ms. The abstract should be placed at the head of the text and should not exceed 5% of the length of the ms.

For Major Papers, the address of each author should appear as a numbered footnote at the bottom of the first page of text.

Authors submitting General Notes should place references in a terminal "Literature cited" section, unless fewer than 5 references are cited in the text. Manuscripts with fewer than 5 references should have internal citations, e.g., (James, Wilson Bull. 83:215–236, 1971) or James (Wilson Bull. 83:215–236, 1971).

More detailed instructions are in "Information for Authors," which follows this announcement.

I believe the above changes in format will strengthen the presentation of material in *The Wilson Bulletin.* They are also designed to make information published in the *Bulletin* more easily accessible by literature search and abstracting services.

As always, I welcome queries from authors concerning style and format during the preparation of mss for submission to the *Bulletin.*—KEITH L. BILDSTEIN, Editor.

INFORMATION FOR AUTHORS

The Wilson Bulletin publishes significant research and review articles in the field of ornithology. Mss are accepted for review with the understanding that the same or similar work has not been and will not be published nor is presently submitted elsewhere, that all persons listed as authors have given their approval for submission of the ms, and that any person cited as a personal communication has approved such citation. All mss should be submitted directly to the Editor.

Text.—Manuscripts should be prepared carefully in the format of this issue of *The Wilson Bulletin.* Mss will be returned without review if they are not properly prepared. They should be neatly typed, double-spaced throughout (including tables, figure legends, and "Literature cited"), with at least 3 cm margins all around, and on one side of good quality paper. Do not use erasable bond. **Mss typed on low-quality dot-matrix printers are not acceptable.** The ms should include a cover sheet (unnumbered) with the following: (1) Title, (2) Authors, their institutions, and addresses, (3) Name, address, and phone number of author to receive proof, (4) A brief title for use as a running head. All pages of the text through the "Literature cited" should be numbered, and the name of the author should appear in the upper right-hand corner of each. The text should begin in the middle of the first numbered page. For Major Papers, the address of each author should be given as a footnote at the bottom of the first numbered page. Three copies should be submitted. Xerographic copies are acceptable if they are clearly readable and on good quality paper. Copies on heavy, slick paper, as used in some copy machines, are not acceptable.

Tables.—Tables are expensive to print and should be prepared only if they are necessary. Do not repeat material in the text in tables. Tables should be narrow and deep rather than

wide and shallow. Double space all entries in tables, including titles. Do not use vertical rules. Use tables in a recent issue of the *Bulletin* as examples of style and format. Tables should be typed on separate unnumbered pages and placed at the end of the ms.

Figures.—Illustrations must be readable (particularly lettering) when reduced in size. Final size will usually be 11.4 cm wide. Illustrations larger than 22 × 28 cm will not be accepted, and should be reduced photographically before submission. Legends for all figures should be typed on a separate page. Photographs should be clear, of good contrast, and on glossy paper. Drawings should be in India ink on good drawing board, drafting paper, or blue-lined graph paper. All lettering should be done with a lettering instrument or adhesive transfers. Do not use typewriter or computer lettering. Designate the top of each illustration and label (on the back in soft pencil) with author's name, ms title, and figure number. Submit 2 duplicates or readable xerographic copies of each figure as well as the original or high-contrast glossy photo of the original.

Authors of accepted papers are urged to submit voucher photographs of their work to Visual Resources for Ornithology (VIREO) at the Academy of Natural Sciences of Philadelphia. Accession numbers from VIREO will then be published within appropriate sections of the paper to facilitate access to the photographs in subsequent years.

Style and format.—The current issue of *The Wilson Bulletin* should be used as a guide for preparing your ms; all mss must be submitted in that format. For general matters of style authors should consult the "CBE Style Manual," 5th ed., Council of Biology Editors, Inc., Bethesda, MD, 1983. Do not use footnotes or more than 2 levels of subject subheadings. Except in rare circumstances, major papers should be preceded by an abstract, not to exceed 5% of the length of the ms. Abstracts should be informative rather than indicative, and should be capable of standing by themselves. Most units should be metric, and compound units should be in one-line form (i.e., cm-sec^{-2}). The continental system of dating (19 Jan. 1950) and the 24 hour clock (09:00, 22:00) should be used.

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Nomenclature.—Common names and technical names of birds should be those given in the 1983 A.O.U. Check-list (and supplements as may appear) unless justification is given. For bird species in Central and South America the *Bulletin* uses the common names appearing in Eisenmann, "Species of Middle American Birds," 1955 and Meyer de Schauensee, "The Species of Birds of South America," 1966. Common names of birds should be capitalized. The scientific name should be given at first mention of a species both in the abstract and in the text.

The editor welcomes queries concerning style and format during your preparation of mss for submission to the *Bulletin.*—Keith L. Bildstein, Editor.

1986 ANNUAL MEETING

The Sixty-seventh Annual Meeting of the Wilson Ornithological Society will be held 17–20 April 1986 at the Holiday Inn in Gatlinburg, Tennessee. This will be the third joint meeting with the host, the Tennessee Ornithological Society. The two-day scientific program will include contributed papers and a mini-symposium on the avifauna of the Southern Appalachians. All-day field trips on 20 April will visit various low and high elevation habitats in the Smokies, including spruce-fir, northern hardwood, and beech gap communities. Many of the resident and short-distance migrant breeding birds will be on territory, and wildflowers will be abundant. Tours for spouses will include cultural and natural history sites. An exhibit of bird art is planned. Chairman of the Scientific Program Committee is Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6. Chairman of the Local Committee on Arrangements is Charles P. Nicholson, Tennessee Valley Authority, Norris, Tennessee 37828. The meeting announcement and call for papers will be mailed shortly.

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